

# Development and Origin of the Respiratory Organs in Araneæ.

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By

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 With Plates 1—7 and 7 Text-figures.
 

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## I. INTRODUCTION.

It is just one hundred years ago that the first anatomical account of the lung-books of Arachnida was published by Meckel ('09), who, like his immediate successors, looked upon these organs as gills, and it was not until 1828 that their pulmonary nature was recognised by Johannes Müller ('28a, '28b) and Straus-Durckheim ('28). The latter was also, I be-



lieve, the first to point out (p. 315) that the lung-books could be regarded as a special form of tracheæ, a view which was later on elaborated by Leuckart ('48, p. 119 note, and '49) and for a time generally accepted, until the appearance of Ray Lankester's paper, "*Limulus: an Arachnid*," in 1881, opened up the probability of the branchial origin of these organs.

While working at certain points in the embryology of a spider some years ago it occurred to me that a more careful and detailed investigation of the development of the lung-books and tracheæ than had hitherto been attempted would probably reveal some points of interest in connection with the origin of these organs, and indeed it soon appeared that two important facts had been entirely overlooked, viz. (1) the appearance of the earliest lung-leaves on the free posterior side of the provisional abdominal appendages quite outside of the pulmonary invagination, and (2) the origin of a considerable part of the tracheæ from ectodermal tendons (entapophyses) and not from lung-books. This latter appeared to me a point of particular interest, as it is the only case, I believe, in which the origin of a trachea from another organ not respiratory in nature can be clearly demonstrated.

My investigations were carried out in the years 1894 and 1895, in the Zoological Laboratory of the University at Berlin, and my thanks are due to Geheimrath Prof. F. E. Schulze for the use of his splendidly equipped laboratory. About one third of the text had already been written and most of the figures drawn when I left Berlin in 1895 for South Africa, where various circumstances prevented the completion of the paper for the press until quite recently.

**Material.**—The material for the development was collected in the neighbourhood of Berlin, and consisted of the embryos and young of *Sitticus* (*Attus*<sup>1</sup>) *floricola* C. K., of which I had an unlimited supply of all the required stages of development. Besides these I examined a small number of

<sup>1</sup> This name has been recently discarded by E. Simon and *Sitticus* substituted in its stead.

embryos and young of *Agelena labyrinthica* and of *Tegenaria atrica*, but the account of the embryology in the following pages applies only to *Attus floricola*, unless the contrary is expressly stated.

The material required for anatomical purposes consisted of adult or subadult specimens of forty-one species mostly obtained in the neighbourhoods of Berlin or Cape Town, as stated in the list given below. The specific determination of the European specimens (except *Tegenaria atrica*) were made from Dahl ('83), but the families and genera are in agreement with E. Simon ('Hist. Nat. Araign.,' 2nd ed.).

#### LIST OF THE SPECIES USED.

(The twenty-nine species marked with an asterisk [\*] were also examined in sections.)

#### Tetrapneumonous Spiders.

Fam. Aviculariidae.

Sub-fam. Aviculariinae.

\**Crypsidromus intermedius*, Paragnay.

*Harpactira atra*, Latr., Cape Town.

Sub-fam. Ctenizinae.

*Stasimopus unispinosus*, Purc., Cape Colony.

*Hermacha* sp., Cape Town.

#### Dipneumonous and Apneumonous (Caponia) Spiders.

Fam. Eresidae.

*Eresus* sp., Cape Town.

Fam. Sicariidae.

\**Scytodes testudo*, Purc., Cape Town.

Fam. Dysderidae.

\**Dysdera* sp., Berlin.

\**Harpactes Hombergi*, Scop., Berlin.

\**Segestria senoculata*, L., Berlin.

## Fam. Caponiidæ.

\**Caponia spiralis*, Purc., Cape Colony.

## Fam. Drassidæ.

\**Drassodes* (*Drassus*) *infuscatus*, Westr., Berlin.  
*D. tessellatus*, Purc., Cape Colony.

\**Melanophora* (*Prothesima*) *Petiveri*, Scop.,  
Berlin.

## Fam. Palpimanidæ.

\**Palpimanus* sp., Cape Town.

## Fam. Theridiidæ.

*Latrodectus geometricus*, C. K., Cape Town.

\**Theridion lineatum*, Cl., Berlin.

## Fam. Argiopidæ.

Sub-fam. Linyphiinæ.

\**Linyphia triangularis*, Cl., Berlin.

Sub-fam. Tetragnathinæ.

\**Pachygnatha Listeri*, Sund., Berlin.

Sub-fam. Nephilinae.

*Nephila* sp., Senegal.

Sub-fam. Argiopinae.

*Argiope clathrata*, C. K., Cape Town.

## Fam. Thomisidæ.

\**Philodromus* (*Artanes*) *fuscomarginatus*, De  
G., Berlin.

\**P.* (*Artanes*) *pallidus*, Walck., Berlin.

\**Tibellus oblongus*, Walck.

## Fam. Clubionidæ.

*Palystes* sp., Cape Town.

\**Clubiona holosericea*, De G., Berlin.

\**Zora* sp., Berlin.

## Fam. Agelenidæ.

\**Argyroneta aquatica*, Cl., Berlin.

\**Textrix lycosina*, Sund., Berlin.

\**Agelena labyrinthica*, Cl., Berlin.

\**Tegenaria atrica*, C. K., Berlin.

*T. domestica*, Cl., Cape Town.

## Fam. Pisauridæ.

\**Pisaura* (*Ocyale*) *mirabilis*, Cl., Berlin.

\**Dolomedes* sp., Berlin.

## Fam. Lycosidæ.

\**Lycosa* (*Trochosa*) sp., Berlin.

\**L.* (*Pirata*) *hygrophila*, Thor., Berlin.

\**L.* (*Tarantula*) *aculeata*, Cl., Berlin.

*L. Darlingi*, Poc., Cape Town.

\**L.* sp., Berlin.

Fam. Salticidæ (*Attidæ*).

\**Sitticus* (*Attus*) *floricola*, C. K., Berlin.

*S.* (*Attus*) sp., Berlin.

\**Marpissa* (*Marpessa*) *mucosa*, Cl., Berlin.

**Biological observations.**—*Attus floricola* fastens its cocoons on dead branches, etc., on the edges of the lakes in the Grunewald, a forest near Berlin, and I have found as many as twenty or thirty cocoons closely packed together in a group at the N.W. corner of Hundekühle See. The number of eggs in a cocoon varies normally from about thirty-five to fifty, and eggs may be found in the cocoons throughout June, July, and the first half of August.

A number laid in captivity on July 12th hatched (i. e. burst the egg-shell) on July 28th and 29th, i. e. after sixteen to seventeen days. At the time of hatching the embryos are still very imperfectly formed and very much resemble *Locy's* fig. 10, except that the legs, which are curved inwards and ventrally, are segmented. The pedipalps are each provided at the base with a small conical tooth, which is broader than high and drawn out at its apex into a tiny brown point. Shortly before hatching the egg-shell becomes stretched and raised on the tips of the two teeth, which then split it across in front of the chelicera.<sup>1</sup>

<sup>1</sup> I also found the two teeth in *Xysticus*, *Tegenaria*, and *Agelena*, the teeth and the part of the cuticula on which they stand being black in the two latter genera. These teeth do not appear to have been previously observed, and they have been recorded in Korschelt and

After hatching the embryos remain motionless for five to six days or even a little longer before the first post-embryonic moult takes place, after which the young spiders acquire the use of their limbs. They are still, however, in a very imperfect condition, especially as regards the eyes. They remain in the cocoons until after the second moult, which takes place sixteen to seventeen days after the first. The young spiders then emerge in a perfect condition, with fully-developed eyes, and have also acquired the definite shape of the adult.<sup>1</sup>

The entire development, therefore, takes from about thirty-seven to forty days, less than half of which number is spent within the egg-shell.

**Treatment.**—The preserving reagent upon which I mostly relied was a hot concentrated alcoholic solution of corrosive sublimate, which I make use of in the following manner: A quantity of sublimate is placed in a small, loosely corked, boiling flask with some alcohol of 70 per cent. and heated over a flame with constant shaking until the alcohol begins to boil. Some of the concentrated solution is then poured into a small tube of about 3 c.cm. capacity, which is immediately corked and suspended by a string in a basin of water heated to 80° C.<sup>2</sup> A few eggs are now dropped in and removed almost immediately afterwards by means of a thin glass rod, which is flattened at one end and here bent at right angles to form a scoop large enough to take out one egg at a time.<sup>3</sup> The sublimate will probably be precipitated during the latter operation, but that does not matter. The eggs are then placed in 63 per cent. alcohol (70 per cent. will

Heider ('92, p. 588). Later on I found a similar black tooth on the base of each pedipalp in the embryo of a Tetrapneumonous spider (*Harpactira atra*) from Cape Town.

<sup>1</sup> Similar phases occur in the development of all other Dipneumonous spiders which I have examined.

<sup>2</sup> A temperature of 70° has much the same effect.

<sup>3</sup> It sometimes happens that the egg-shell bursts, in which case the embryo is destroyed by the violent action of the reagent. As a rule, however, it remains intact and only just sufficient reagent penetrates to preserve the embryo.

do as well) for one hour, the alcohol being changed several times, then for one to two hours in 78 per cent. alcohol, and finally in 93 per cent. and absolute alcohol. Chloroform was used for embedding in paraffin and the sections were stained on the slide in alum carmin, which I found the most suitable for them.

A number of embryos were also preserved in a hot aqueous solution of corrosive sublimate (concentrated at the ordinary temperature) for the purpose of control. I did not, however, require to make much use of these embryos, which could not compare with the others in point of preservation.

The great disadvantage attached to the use of plain hot water or hot aqueous solutions, which are the methods hitherto usually employed in spider embryology, lies in the circumstance that the embryonic tissues take the appearance of a syncytium when so preserved. It accordingly becomes difficult to distinguish between two or more epithelia in contact, the several layers of nuclei being then usually the only feature by which the nature of the tissue can be guessed at rather than recognised.

I devised the hot alcoholic sublimate method described above only after repeated experiments. It has the merit of rendering the contours of the cells much more distinct, so that not only the boundary line between two epithelia in contact, but generally also the boundary lines between adjacent cells within an epithelium becomes recognisable.

In the sections these cell-contours may appear in the form of fine dark lines or they may be indicated merely by a difference in the staining between the protoplasm of adjoining cells or by the presence of paler lines between the cells, as if these had been slightly drawn apart.

As the appearance of the protoplasm was of minor importance, but the contours of the epithelia and their cells of the greatest importance in my investigations, I have for convenience represented the contours in the figures by dark lines, by which, of course, I do not intend to imply that regular cell-walls are present.

I found it quite impossible to obtain an accurate idea of the rudimentary lung-books and tracheæ in the embryos, except by means of reconstructions, of which extensive use was made. For the complicated lung-books a large number of the ordinary reconstructions with wax tablets were made (thickness of sections  $5.82\mu$ , of wax tablets 2 mm.; magnified 343.7 diameters), but for the simpler tracheæ the following method was employed:

A sheet of transparent paper is placed over another of white paper ruled with a series of parallel lines 2 mm. apart. The width of the organ to be reconstructed magnified the required number of times (343.7 times for sections  $5.82\mu$  thick), is measured with a pair of compasses in each section and marked off on the parallel lines, each of which represents a section. When all the sections have been marked in this way on the transparent paper the outlines of the organ will be obtained in their correct proportions. This method is much quicker than the other and very suitable for reconstruction in outline from transverse sections of any bilaterally symmetrical organ of simple form, such as the embryonic tracheæ in the later stages (figs. 28 and 29). By drawing a line down the middle of the paper at right angles to the parallel lines to represent the median line of the body, and marking each transverse section symmetrically on each side of this line, the symmetry of the reconstructed organ will be preserved.

## II. GENERAL ORIENTATION.

**Lung-books.**—A typical well-developed lung-book of a Dipneumonous spider has the following parts (figs. 20 and 21):

(1) A more or less transverse spiracle (*sp.*) or stigma placed laterally at the junction of the ventral and lateral surfaces of the second abdominal segment along its hind margin (text-fig. 1).

(2) A short flattened tube leading forwards from the spiracle into the body in a slightly upward and medial direc-

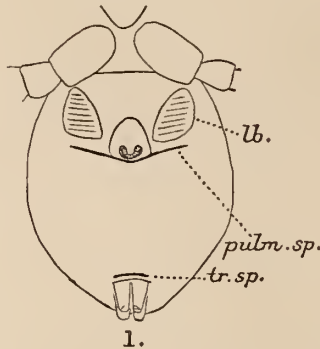


tion, forming a stalk or pedicel (*ped.*) to the whole lung-complex. This opens into—

(3) An elongated-lanceolate hollow band, the pulmonary sac (ante-chamber or vestibule, *pulm. s.*), which runs from just in front of the medial angle of the spiracle at first in a dorso-lateral direction, but becomes procurved at a greater or less distance beyond the lateral angle of the spiracle to form the horn (Schneider, *h.*) and terminates in a short, blind, apical pouch (*ap.*).

(4) A series of long, flattened, hollow pouches (saccules, *s.*), which are triangular in shape, like a flattened butterfly-net, generally horizontal, and placed one over the other in a

TEXT-FIG. 1.



*Attus floricola*. Ventral surface of abdomen. *lb.* Pulmonary operculum. *pulm. sp.* Pulmonary spiracle. *tr. sp.* Tracheal spiracle. Magnified 13.

slightly imbricating manner (each being slightly more lateral than the one below it), like the leaves of an open book. The saccules, being invaginations of the anterior wall of the ante-chamber, communicate with its lumen by their open posterior ends, which form a series of parallel slits, like an oven-grate (Bertkau), extending obliquely across the entire anterior surface of the ante-chamber, including the corresponding ventral surface of the procurved horn, being absent only from the small apical pouch of the latter.<sup>1</sup>

<sup>1</sup> In some text-books, e. g. Korschelt and Heider ('92, p. 605, fig. 382)



All these parts, being hollow, contain air in direct communication with the external atmosphere. The partition walls between the air-spaces of adjacent saccules, I shall term the "septa."<sup>1</sup> The dorsal side of each septum is studded with numerous, simple, blunted spines, which keep the lumens of the saccules open, while the walls of the ante-chamber (including its fenestrated anterior wall and the apical pouch of the horn), are covered with peculiar hooped spines (spines with anastomosing apical branches). The pedicel is for the most part unspined.

The two spiracles are generally united by a transverse fold, the epigastric or interpulmonary fold (*interp. fld.*), which also connects the two pedicels and the extreme medial corners of the two ante-chambers (see text-fig. 1). The lumens of the latter at the same time communicate by the interpulmonary canal of communication (*can.*), or passage with hooped spines in the upper edge of the fold.

Further remarks on the lung-books of the adult are given on p. 41, and an historical account of the literature will be found at the end of the paper.

**Tracheæ.**—The usual form of tracheæ in a Dipneumonous spider has the following parts (figs. 21, 25 and 31):

(1) A median, transverse, ventral spiracle (*sp.*), placed on the hind margin of the third abdominal segment usually just before the spinners (text-fig. 1).

the procurved horn is wrongly represented as having no saccules opening into it.

<sup>1</sup> In order to avoid ambiguity I have substituted the terms "sacculi" and "septa" in place of the old terms "leaves" and "lamellæ." The older writers almost invariably meant to indicate the saccules when they used the term "leaves" (*fenillets*, Blatter), but since about 1881 the term has generally been employed for the septa, like the term "lamellæ." Neither term, however, has at present any definitely recognised use. Thus "lamelles" signifies the septa with MacLeod ('84), but only one of the layers of a septum with Berteaux ('89), whose term for a whole septum is "lame," while "feuillet" signifies a septum with Schimkewitsch ('84) and Plateau ('86), but a saccule with Schneider ('92).

(2) A short, flattened chamber (vestibule, *vest.*), leading forwards and upwards from the spiracle into the body and giving off at its anterior or deepest part—

(3) A pair of medial (*m.tr.*) and a pair of lateral tracheal trunks (*l.tr.*), which may again give rise to tracheal branches (*br.*, fig. 21), the finest of these being the tracheal tubules (*tr.tub.*, fig. 31). The trunks and branches are lined with anastomosing spines (more rarely with spiral threads only), but the fine tubules have only spiral threads.

The anterior or deepest part of the cavity of the vestibule is always widened to form a transverse canal of communication (*can.*) or passage with hooped spines, connecting the cavities of the tracheal trunks. The remaining or smooth portion of the vestibule forms a stalk or pedicel (*ped.*) to the whole tracheal system, and is supported on each side by chitinous thickening or rod (*rd.*).

### III. HISTORICAL (DEVELOPMENT).

**Development of the lung-books in Arachnida.**—Metschnikoff ('71) gives an account of the development of the lung-books in scorpions, and observes that they arise as ectodermal invaginations just behind the four posterior pairs of abdominal appendages, which latter subsequently atrophy. Towards the end of the embryonic period the folds in the pulmonary sacs appear.

Salensky ('71) was the first to study their development in Araneæ, and believed that the lung-books were formed by the invagination of the abdominal appendages (teste Jaworowski, '94, p. 55).

Bertkau ('72) showed that in the young spider, after the completion of the embryonic period, the lung-books continue to develop, new leaves being added at the growing dorso-lateral end, each new leaflet arising next to the one previously formed.

Locy ('86) gives a detailed description of the later stages

in a spider (*Agelena nævia*), and he is the first to give an account of the transformation of the embryonic epithelial foldings into the definite pulmonary septa (lamellæ) with their chitinous coverings. According to him the lung-books arise as a pair of invaginations late in the period of the reversion, but he makes no mention of their connection with appendages.

Bruce ('86a, '86b, '87) is of opinion that the pulmonary folds in spiders are formed on the anterior surface of the first abdominal appendage, which subsequently becomes involuted, so that its anterior surface with the folds now faces the posterior end. Probably two abdominal appendages are invaginated for each lung-book.

Schimkewitsch ('87; also in '86a and '86b, teste Jaworowski, '94) states that the lung-book arises as an invagination of the ectoderm and forms a true trachea, consisting of a main trunk divided into five branches, in the embryo of *Lycosa saccata* just before hatching. Recently, however, Schimkewitsch (:06, pp. 45, 46, footnote) has withdrawn this interpretation.

Kowalevsky and Schulgin ('86) merely note that the pulmonary sacs in the scorpion (*Androctonus ornatus*) arise as simple invaginations into a space containing plenty of blood.

Morin ('87) found that the lung-books in the spider (*Theridion*) arise from a pair of ectodermal invaginations at the base of the first pair of abdominal appendages, which themselves become the lung-opercula. In his later paper ('88) he appears to have given more details of the formation of the lamellæ, of which those nearest the operculum are furthest developed (teste Jaworowski '94, pp. 57 and 58).

Laurie ('90) states that in the scorpion (*Euscorpion italicus*) the four last pairs of abdominal appendages are pushed in on their posterior part, so as to form shallow, cup-like cavities, which later on are divided up by lamellæ growing down from their upper ends (pp. 125 and 127). A later stage with lamellæ is also described (p. 129). In a later paper ('92) he deals with the development in *Scorpio fulvipes*.

Kishinouye ('90) confirms the statement regarding the lung-books and the opercula contained in Morin's earlier paper ('87), and adds that that wall of the invagination which faces the distal end of the appendage is much thickened, filling the interior of the appendage, the cells becoming after a while arranged in parallel rows to form the septa. He examined *Lycosa*, *Agelena*, *Theridion*, *Epeira*, *Dolomedes* and *Pholcus*.

Simmons' ('94) paper is the most important that has yet appeared on the development of the spider's lung-books, and was based on embryos of *Agelena naevia* and *Theridion tepidariorum*. He confirms Morin's and Kishinouye's statements regarding the formation of the pulmonary invagination, and was the first to describe and figure an early stage of the formation of the pulmonary septa (lamellæ), which he states arise as infoldings upon the posterior surface of the abdominal appendage in the same manner as described by Kingsley for the gills of *Limulus*.

Jaworowski ('93 and '94) describes the presence in a spider embryo (*Trochosa*) of embryonic tracheæ, which ultimately becomes rudimentary, excepting the portion adjoining the spiracle. The wall of this portion is thrown into folds and persists as the lung-books. The author thus totally differs in some most important points from all his predecessors. These tracheæ arise from invaginations under the abdominal appendages, the latter becoming the opercula ('95, p. 43). Jaworowski also gives a valuable account of the formation of the definite pulmonary septa out of the folded embryonic epithelia.

According to Laurie ('94) the embryonic abdominal appendages are not paired in the Pedipalpi, but stretch right across the abdomen, and in *Phrynus* the lung-books evidently arise as foldings of the posterior wall of an appendage.

Brauer ('95) confirms Metschnikoff's and Laurie's observations on the earlier stages of the pulmonary invaginations at the base of the four posterior pairs of abdominal appendages

in scorpions, and gives the best account of the early stages of the pulmonary folds (in *Euscorpium carpathicus*).

In my own paper ('95) the appearance of the earliest pulmonary folds on the free posterior side of the first pair of abdominal appendages in *Araneæ* is described.

Sophie Pereyaslawzewa (:01) investigated the earliest appearance of the lung-books in *Phrynidæ* in *Phryniscus bacillifer* and the later stages in *Damon medius*. According to her the lung-books are formed from the third and fourth abdominal appendages, which belong to the third and fourth abdominal segments (p. 194). The outer integument, the cuticula of which is regularly wrinkled (fig. 61), is deeply infolded into the body behind the third and fourth appendages to form the lung-sacs, the grooves in the invaginated wrinkled surface deepening to form the sacculæ, while the ridges become the septa (pp. 248-252). The embryonic septa are also described (p. 262) and figured (fig. 69).

Gough (:02) states that the lung-books in an embryo of a Pedipalp (*Phrynid*) belong to the first and second abdominal appendages. The author gives no further account of the development of the lung-books, but merely states that it does not differ from that in other *Arachnids* (p. 616).

Schinkewitsch (:03, :06) gives a more detailed account of the development of the lung-books in *Thelyphonus caudatus*. According to him the lung-books are formed from pulmonary sacs or invaginations at the base of appendages, which are placed on the hind margins of the second and third abdominal somites. The lung-leaves arise as folds in the lower wall of this sac, and later on the leaves, which were formed in the sac, come to lie outside of it on the posterior side of the appendages so that the sacculæ then open to the outside instead of into the sac (fig. 46). Several sections of later stages of the lamellæ are figured.

Sophie Pereyaslawzewa (:07), in a posthumous memoir, describes and figures some interesting stages in the development of the lung-books of a scorpion (*Androctonus ornatus*) from the material left by Kowalevsky and Schulgin.

According to her the invagination which forms the pulmonary sac is situated on the anterior edge of the lateral part of the base of an abdominal appendage and is apparently unconnected with the latter (p. 177).

**Development of the tracheæ in Araneæ.**—Schimkewitsch ('87) states that the tracheæ in *Lycosa saccata* arise by invaginations of the ectoderm. In his Russian paper ('86a) he gives a figure of a developing trachea (*ect*, fig. 29A), without, however, recognising it as such.

Kishinouye ('90) observed an ectodermal invagination in various spiders in the basal part of the second abdominal appendage on the interior side. This invagination forms a deep tube at the time of hatching and the author calls it an "abortive trachea."

Simmons ('94) found the same invagination in *Agelena nævia* and *Theridion tepidariorum*, and in addition what he considers to be aborted lung-leaves.

Finally, in my abstract ('95) of the present paper the origin of the greater part of the tracheæ in *Attus floricola* from ectodermal tendons is stated in outline.

#### IV. THE PROVISIONAL ABDOMINAL APPENDAGES IN THE EMBRYO OF *ATTUS FLORICOLA*.

The description begins with the stage<sup>1</sup> immediately preceding the appearance of the pulmonary folds (stage 1, *St.* 1). The embryonic band has attained its greatest length, and the process known as the reversion is about to commence. A sagittal section (Pl. 1, fig. 4) through the abdominal region shows eight abdominal segments with coelomic sacs. The first abdominal (seventh post-oral) segment bears no appendages in this species, but the following four (eighth to eleventh post-oral) are each provided in their posterior region with a low, flat-topped,

<sup>1</sup> Corresponding to the stage in Korschelt and Heider, p. 581, fig. 369, and to Loey's Pl. ii, fig. 8, and Balfour's fig. 6. A list of the various stages and of the figures referring to each is given in the explanation of the plates.



provisional appendage (*ab. app.* 1-4) in successive stages of growth, that of the eleventh segment being the smallest and that of the eighth the largest.

The segments are marked off from each other by distinct transverse grooves, which are shallow, except immediately behind the appendages, where they are considerably deepened (*gr.*), and where the ectoderm forms a distinct post-appendicular fold, projecting at right angles, or nearly so, to the general surface into the body. The posterior wall of this fold is comparatively thin, like the adjacent epithelium of the following segment, but the anterior wall is much thicker, being, in fact, a direct continuation and a part of the posterior wall of an appendage, as I shall presently show.

A similar post-appendicular infolding (as distinct from the pulmonary sac to be described later) appears to be also found in *Limulus* (Kingsley, '85). In the older spider-embryo those of the posterior pairs of appendages serve as places of attachment for the ventral longitudinal muscles of the abdomen.

The deep infoldings behind the first pair of abdominal appendages extend from the medial end of the hind margin of each appendage nearly, but not quite, up to the extreme lateral end, and, moreover, the lateral part of the infolding (*gr.*, fig. 7A) is always slightly, but distinctly, deeper than its medial part (*gr.*, fig. 7). These two figures represent the appendages just before the earliest appearance of the rudiments of the lung-books.

#### V. THE DEVELOPMENT OF THE LUNG-BOOKS.

**Stage with two pulmonary furrows** (stage 2, *St.* 2).—The appendages of the pulmonary or eighth post-oral segment undergo considerable changes in passing from the stage just described to the next one, which I shall term the "stage with two pulmonary furrows." Fig. 1 is a transverse section of this stage, and shows that the appendages are still near together, although the reversion has commenced. This stage

follows so quickly upon the last that it is at first very puzzling to make out the changes accurately, but with the aid of numerous reconstructions in wax I have been able to ascertain the more important phases with certainty.

Fig. 14 is a sketch made from such a reconstruction, and represents the typical appearance of the right appendage seen somewhat from behind. Its distal surface is flat and often, although not always, distinctly transverse. Measured at the base, however, the breadth of the appendage is about equal to the antero-posterior diameter, and remains in this relation throughout the later stages. Seen from the distal surface the appendage appears distinctly four-sided, with its posterior side placed transversely to the embryonic band.

Fig. 8 is another reconstruction made from a series of longitudinal sections cut parallel to the principal axis (*pr. ax.*, fig. 1) of the appendage, and a number of sections from this series are given in figs. 8A-8H, the positions of the sections being indicated by the vertical lines in fig. 8.

The first point to be noticed is the subsidence of the epithelium (*ep.*, figs. 8A-8G) lying immediately behind the first abdominal appendage and forming the posterior lip of the post-appendicular groove<sup>1</sup> (*gr.*, in stage 1, fig. 7). The two lips of the latter thus become drawn completely apart along its whole length, so as almost to obliterate the groove as such (except at a single place to be mentioned presently) and lay free the whole posterior side of the appendage. In its median half the former bottom of the groove is now indicated only by a shallow furrow (*gr.*, figs. 8A-8D), which at the same time marks what in the previous stage (fig. 7) was the base of the posterior side of the appendage. This shallow furrow behind which the subsidence was greatest is more or less curved owing to a shifting backwards of the tissue in which it lies (*gr.*, fig. 14), so that the posterior side of the appendage comes to slant in its medial part at base (*sl.*, figs. 8A-8D,

<sup>1</sup> A corresponding subsidence also takes place anteriorly to the first appendage, causing the obliteration of the groove between the seventh and eighth segments.



and 14) much more than was the case in the previous stage, where the groove was straight and transverse. The angle of the slanting surface varies, the latter being in some embryos nearly perpendicular, in others nearly parallel to the adjacent body surface (*ep.*), and in the latter case the curved furrow may entirely disappear. The above will become clear by comparing figs. 8b and 9 of this stage with the corresponding section (fig. 7) of the previous stage.

In the second place we notice a little pocket-like cavity (*pulm. s.*, figs. 8 and 14) extending from the middle of the base behind in a lateral direction for about one third of the breadth of the appendage. This cavity, which we may term the pulmonary sac, is practically all that remains of the once extensive post-appendicular groove, and is to be considered as a portion of the latter which had become especially deepened and so escaped the obliteration which befel the rest of the groove—for a subsidence has also taken place in the tissue immediately behind the pocket. (Compare fig. 8c with the corresponding section, fig. 7A, of the previous stage.)

The pulmonary sac was first described and figured by Metschnikoff ('71) for the scorpion and was found by most subsequent investigators, but generally in a later stage of development.

The cells which form the wall of the sac undergo from now on repeated division (fig. 8c), causing the sac to grow rapidly, at first in a forward direction in the form of an in-pushing under the appendage, but later on in a latero-dorsal or dorsal direction (fig. 16). The anterior wall of the pulmonary sac yields the cell-material for all the lung saccules, except the first two, whose appearance forms the third and most important point to be noticed in this stage.

On the medial half of the posterior side of the appendage there appear two parallel furrows of varying length (*f. 1, f. 2*, figs. 8 and 14). These are the first beginnings of the two oldest saccules of the lung-book. They are never transverse but always incline to the longitudinal axis of the appendage

at varying angles. The first or medial furrow (*f. 1*) is always much the deeper and extends from near the medio-posterior angle of the base of the appendage in a latero-distal direction. As a rule when the posterior face of the appendage is strongly inclined, the furrow takes a more transverse direction and does not then reach the distal surface (as in figs. 8 and 14), but when the posterior face is less inclined, the furrow takes a direction more nearly parallel to the axis of the appendage, extends right up to the distal surface of the latter, and comes to be situated on its medio-posterior corner (fig. 10). In such cases, in fact, it is sometimes more on the medial than on the posterior side of the appendage. The second furrow (*f. 2*) appears almost simultaneously with the first, and is situated between the latter and the base of the appendage, so that its medial end terminates on the proximal side of the lateral part of the first furrow. It never extends right to the base nor to the distal surface of the appendage, and if produced medially would run proximally to the first furrow.

Compared with the preceding stage the medial half of the appendage has developed considerably and is sharply set off from the body surface. Further, in its lateral part (fig. 8*g*) the anterior side has become much more inclined than in the preceding stage (fig. 7*A*), so as to be parallel to the slanting anterior wall of the pulmonary sac. In longitudinal sections through this part (fig. 8*g*) the appendage has the false appearance of being directed backwards, and this becomes still more marked in later stages (as for instance figs. 12 and 16*c*). That this appearance is deceptive and merely due to the pulmonary sac will be readily seen if it be remembered that fig. 8*g* is a section lying between the sections fig. 8*f* and fig. 8*h*, and fig. 16*c* a section between fig. 16*a* and fig. 16*d*. The main axis of the appendage remains in all cases at right angles to the body.

**Stages with three or more pulmonary furrows** (stages 3 to 5).—The third furrow (*f. 3*, fig. 16) appears at the middle of the base of the posterior side of the appendage. It is

parallel to the others and lies partly inside and partly outside of the pulmonary sac. Its medial part lies proximally to the lateral end of the second furrow, and, in some cases at least, is continuous with the lateral end of the curved furrow mentioned above (*gr.*, fig. 14), which limits the appendage posteriorly. The fourth furrow (*f.* 4, fig. 16) and all subsequent ones lie wholly within the pulmonary sac and appear successively as oblique grooves in its anterior wall, all more or less parallel to those already formed and with the medial ends of each lying on the proximal side of the lateral part of the previously formed furrow.

After the appearance of the first two furrows the appendages rapidly move from a ventral to a lateral position owing to the reversion of the germinal band, and it is necessary to bear in mind that we must substitute the terms "dorsal" and "ventral" for "lateral" and "medial" after the lateral position has been reached.<sup>1</sup>

Figs. 1-3 will make this clear. Fig. 1 is the position at the end of the 2-furrow stage; fig. 2 that at the end of the 3-furrow stage, and fig. 3 represents the position from the end of the 4-furrow stage, and here the appendages remain till near the close of the embryonic period. The whole segment which bears the appendage participates in this wandering, and the position of the appendage relatively to the adjacent surface is, of course, not affected by the movement.

It will be observed that the youngest furrow (fig. 3) is the most dorsal one, and, if produced, would lie on the proximal side of all the older ones.

The pulmonary sac increases hand in hand with the formation of new furrows, almost filling out the dorsal part of the hollow of the appendage. At the 5-furrow stage its blind end grows as a tube with a considerable lumen in an upward or dorsal direction, raising up the outer epithelium as it pushes its way underneath (see figs. 16, 16D, 16E).

<sup>1</sup> For the sake of uniformity and in order to facilitate comparison between them, the sections of the earlier and later stages of the appendages have been drawn in the same positions throughout.

**Formation of the spiracle.**—After the appendage has attained its greatest elevation (generally late in the 3-furrow stage) the whole region between the three oldest furrows begins to sink below the level of the appendicular posterior surface by a forward movement, causing it to be over-topped by the distal edge of the appendage (fig. 16A). This sinking movement, which must not be confounded with the formation of the pulmonary folds described further on, commences next to the pulmonary sac, and the latter thus comes to include first the third furrow (fig. 16B), then the second, and finally the first, while the common opening becomes the spiracle (*sp.*, fig. 13, which compare with figs. 13A and 13B of the same series).

Meanwhile that portion of the body epithelium which lies immediately in front of each of the four appendages in a row becomes absorbed into the anterior side of the appendage (compare figs. 4, 5, and 6), so that the four appendages appear closer together, while the original opening of the pulmonary sac comes to lie at the bottom of the groove so formed between the first and second appendages.

The lateral (afterwards dorsal) end of the spiracle is the first to be formed, and is already clearly defined immediately after the appearance of the pulmonary sac (fig. 14). The progressive development of the lateral part of the spiracle may be followed in figs. 8G, 12, and 16C. In the latter embryo the surface posterior (fig. 16C) and dorsal (fig. 16D) to the lateral end of the spiracle is almost on a level with the distal surface of the first appendage. The medial (later ventral) region of the spiracle remains open and undefined for a much longer time.

**Sinking of the appendage.**—This is a very simple process and begins about the 5-6-furrow stage (*St.* 5). The anterior and ventral sides become more slanting, so as to pass, like the dorsal side, more and more gradually over into the adjacent body surface, while the appendage itself decreases in elevation and sinks gradually into the body, until finally only a slight convexity in front of the spiracle marks its former position. (Compare fig. 13B, with five pulmonary furrows,

with the corresponding section, fig. 17, of a much later stage.)

**Formation of the pulmonary saccules.**—Next to their position on the posterior side of the appendage, the precise manner in which the saccules begin to form is the point of greatest interest and importance, when considered with regard to their possible direct origin from gill-lamellæ. I have been successful in obtaining a number of excellent sections through the region in question, showing the cell-boundaries with perfect distinctness. The position of these and of the nuclei of each individual cell have been drawn with the aid of a drawing apparatus in the sections figured in the plates, which are in this respect exact reproductions of the original sections (see p. 8).

The three figures 7, 9, and 8c represent longitudinal sections, cut parallel to the axis of the appendage, and, as nearly as possible, through the same region of the latter, in each case indicated by the line marked (*fig. 8c*) in fig. 8. All these sections are through the region in which the first furrow appears, and represent three consecutive phases following close upon one another.

In the youngest stage (fig. 7) no trace of the furrow is apparent, and the appendicular epithelium is composed entirely of elongated cylindrical cells.

In the next stage (fig. 9), however, the distal wall of the oldest pulmonary sacculæ has appeared, and is seen still better developed in fig. 8c. The formation takes place as follows: A cleft (*cl. 1*) in the epithelium appears on its internal surface at the junction of the posterior and distal sides of the appendage, while a similar cleft (the first pulmonary furrow, *f. 1*) is formed almost simultaneously on the outer surface. The cylindrical cells between these two clefts immediately begin to shorten to about one-half of their former length and rearrange themselves as a one-layered epithelium, whose basal and free surfaces are now represented by the internal and external clefts respectively.

The proximal surface of the first pulmonary furrow is still

bounded by the original cylindrical cells (figs. 8B and 8C). In these two figures we see, however, the commencement of a second internal cleft (*cl.* 2) and a second external furrow, the latter being the second pulmonary furrow (*f.* 2). In a later stage the cells between the second internal cleft and the two external furrows are seen in the process of shortening to one half of their former length in order to re-arrange themselves to epithelia having this cleft and the two furrows for their basal and free surfaces respectively (figs. 10 and 11).

The walls of the oldest saccule, embracing the first pulmonary furrow between them, and the distant wall of the second saccule, are, therefore, now present. In a similar manner the proximal wall of the second saccule and the walls of all subsequent saccules are formed (fig. 15).

The external pulmonary furrows are always provided with a distinct lumen, cutting deep into the sides of the appendage and sac, and they have been thus figured by Simmons, who was, I believe, the first to observe them. The internal clefts, on the contrary, have no real lumen whatever, and are indicated on the visceral surface of the epithelium by slight grooves only.

The process described above may be summarised as follows : The cells of the epithelial region which contains the pulmonary furrows shorten and re-arrange themselves in the form of a folded epithelium, which has one half the thickness of the original epithelium and occupies about the same total volume.

By repeated cell-division the folded epithelium expands in such a manner that all those folds which are directed inwards and which contain a pulmonary furrow between their walls grow into and ultimately fill out the cavity of the appendage (figs. 10 and 16A). Each hollow pouch thus produced gives rise, of course, ultimately to a hollow air-containing saccule, while the outwardly directed folds comprised between two pulmonary furrows ultimately form the septa between the air-compartments of the lung-book. The



oldest saccule is the first to grow into the interior, while the others follow in turn in the order in which they were formed.

Simmons ('94) is, so far as I am aware, the only author who has described and figured the earlier stages of the formation of the saccules in spiders. He gives two figures of sagittal sections from embryos of the same age, one (fig. 6) showing five and the other (fig. 5) two pulmonary furrows. The position of these two furrows in the latter figure shows that they are not the two oldest, the others having apparently been missed by the section, which is probably of about the same stage as his fig. 6. Simmons' account is as follows: The outer wall of the pocket "has its ectoderm thrown into folds," the nuclei in this ectoderm "being rather irregularly arranged, the pulmonary ingrowths [i. e. the furrows] forcing their way between them." The more distal gill-lamellæ (by which the author means the septa) are the oldest, as in *Limulus* (p. 217). Simmons' paper is dealt with again further on (p. 36).

**Comparison with the gill-books of *Limulus*.**—It would be profitable here to institute a comparison with the gill-books of *Limulus*.

According to the description and the figures of Kingsley ('85), the gill-leaves of the American *Limulus* arise as outgrowing folds of the epithelium of the posterior side of the appendages, their formation being accompanied by a slight in-tucking of the epithelium between them, and taking place in the same order as the pulmonary saccules in spiders. The epithelial walls of each outwardly directed fold are, however, not in contact along their basal surfaces, and have apparently not been suddenly reduced in thickness, thus differing in these two points from the rudimentary lung-books.

In the Japanese *Limulus* the process appears to be somewhat different. According to Kishinouye ('91), the proximal portion of the appendage is much thicker than the distal portion and is provided with many transverse furrows or invaginations, the tissue between two furrows giving rise to a gill-lamella. At any rate both forms agree in one main

point, namely, that the out-growths or out-foldings are accompanied by an invagination of the ectoderm between them in the earliest stage.

Now, in the case of the rudimentary lung-books in spiders, as summarised on pp. 17-20, it is evident that the pulmonary folds cannot be considered as due to simple out-foldings or in-foldings of an epithelium whose thickness was that of the walls of the folds, as is the case in the American *Limulus* at least. On the contrary, they arise by a peculiar process, which results in the transformation of a very thick but even epithelium into a folded one of one half the thickness, but occupying the same volume, and unaccompanied, therefore, by any out-growth or in-growth at first.

I am of opinion that these two modes of forming a folded epithelium are not fundamentally different, for the one may be readily derived from the other. On the contrary, I believe that the method which obtains in the spider is merely an abbreviation of some such process as occurs in the American *Limulus*, being the most convenient one for rapidly throwing a limited area of a very thick epithelium into folds, for this could not easily be done by ordinary folding, as the breadth of the area in question is only equal to the thickness of the epithelium itself. Which of the two methods was the original depends, of course, on the thickness of the appendicular epithelium in the common ancestor, and is a question of but secondary importance. The Japanese form, according to the description of Kishinouye, appears to bear some resemblance to the spider in the origin of the respiratory lamellæ.

The result of the folding in *Limulus* and the spider are at first practically the same in each case, namely, an undulating folded epithelium, and it is only in the subsequent growth of the folds that a real difference between the two cases becomes apparent. For in each the epithelial cells multiply by division in such a manner that the walls of the folds expand and grow, in the case of the spider, into the interior of the appendage, but outwards and away from the latter in



*Limulus*. We should have no difficulty in imagining a case in which the cells divided so as to cause the folds to expand simultaneously in both directions, and the result would be a structure intermediate between the gill and the lung-book.

The foregoing paragraphs lead up naturally to the simple and ingenious hypothesis first put forward by Kingsley ('85) to explain the derivation of the lung-books from gill-books (see Kingsley's explanatory figs. 18-20). He simply assumes that simultaneously with the sinking of the whole organ the inwardly directed folds of the gill-books became exaggerated, while those directed outwards correspondingly decreased. In this way an intermediate type of respiratory organ would first be obtained, representing the condition in the animal when it was leaving the water and seeking a terrestrial life. Finally, the lung-book type would be reached by the complete suppression of any tendency of the folds to grow outwards.

Now, from a morphological point of view there should be no difficulty in accepting this hypothesis. The passage from a gill-lamella with three free outer edges to a lung-septum with only one such edge is perfectly simple and easy to imagine. It now really constitutes the only assumption not directly proved ontogenetically which we have to make in deriving the Arachnid lung-book from a Limuline gill-book. For the two remaining conditions necessary for such an origin, namely, the appearance of the oldest septa on the free posterior side of the appendage and the subsequent subsidence of the latter, are observed embryological facts. To return to the first point, the ontogeny, although it does not exactly prove it, furnishes us, nevertheless, with some evidence which tends to show that the folds were originally designed to grow outwards and not inwards. For, so far as I could make out, the two walls of the most distal septum or outwardly directed fold are formed simultaneously, and followed later by the simultaneous appearance of the two walls of a second fold also directed outwards, and so on (see fig. 11). It cannot be denied that each such fold, on its first

appearance, creates the impression that it was designed and is about to grow outwards, and one is perhaps justified in asking why, if the saccules were originally derived from trachea-like invaginations, the two walls of a saccule do not appear simultaneously as we should expect from a fold originally designed to grow inwards? I do not, however, wish to attach too much importance to this point, as it is very difficult to ascertain with certainty, and would not even then constitute a clear proof either way.

Passing to the physiological side of the question, one benefit derived from the sinking of the gill-leaves into the appendage and of the latter into the body would, of course, as Kingsley says, be protection from the increased wear and tear incidental to terrestrial motion. The delicate gill-leaves with the three unattached edges would be very liable to injury when deprived of liquid support, while a lung-septum, having only one unattached edge, is perfectly secure. At first, no doubt, the gill-leaves would be very sensitive to evaporation, and the cavities between their basal portions in the intermediate stage (fig. 19 in Kingsley, '85) may have formed convenient reservoirs for retaining water to moisten the respiratory surfaces during terrestrial excursions.

Various other theories have been suggested by different authors (Milne-Edwards, '72, p. 56; Ray Lankester, '81, '85a and '85b; MacLeod, '82 and '84; Laurie, '92 and '93) to explain how gill-books like those of *Limulus*, may have been converted into lung-books, but none of them correspond exactly to the embryological facts, so I shall not consider them further in this paper.

**Later development of the pulmonary saccules.**—I resume the description at the 5-6-furrow stage represented in figs. 13-13B and 16-16E. The interior of the appendage has become nearly filled out by the ingrowing saccules, which push before them the intra-appendicular part of the cœlom and ultimately occupy its place. They continue to grow till the anterior side of the appendage is reached. The oldest saccules are still the longest, but are exceeded in breadth by

the younger ones (fig. 13B)—so much so, indeed, that in the dorsal region the latter project for at least half their mass into the body cavity, while the oldest saccules are still entirely contained within the appendage (a condition still apparent at the time of hatching, fig. 17).

The plane of each saccule is still an inclined one, slanting upwards anteriorly, owing to the presence of the genital duct in the now ventral (originally medial) portion of the appendage. When, in later stages, the duct has migrated elsewhere, the saccules come to lie horizontally and parallel to the ventral side of the appendage (figs. 17 and 18). A slight twist in the plane of a saccule may always be noticed in the 5-6-furrow stage, by which each becomes distinctly more horizontal in its anterior region (fig. 13B) than at the orifice (fig. 13A). This twist does not seem to be retained throughout all subsequent stages.

From the 5-furrow stage until the period when the cuticula and the lacunæ first appear in the lung-books the latter present various characteristics, best studied in transverse sections, such as fig. 13B. The ventral wall of each of the saccules (*s.* 1, *s.* 2, etc.), is distinctly thicker than the dorsal wall, its cells being more cylindrical and more numerous, its nuclei more oblong and situated nearer the ventral (basal) ends of their cells, which thus come to have more protoplasm at the free (dorsal) ends than do the corresponding (or ventral) ends of the cells of the dorsal wall. The saccules are each provided with a considerable cavity, but between the closely appressed walls of two adjoining saccules no lumen whatever is found.

With the appearance of the chitinous structures and the blood-lacunæ at the end of the reversion a great change takes place in the appearance of the walls of the saccules, the older ones being, as usual, those first affected. There appear between the walls and cells of two adjoining saccules irregular spaces (*lac.*, figs. 17 and 18), which are at first small, but rapidly enlarge and communicate with one another and with the blood-cavities on the medial and lateral sides of the lung-

book, thus forming a passage for the blood and blood-corpuscles (*bl.c.*) from the one side to the other. All mitoses definitely cease in such saccules, although they are common enough in the previous stages, as well as in younger not yet chitinised saccules of all subsequent stages. The two adjacent walls do not, however, lose contact with one another, for each cell of a dorsal wall of a saccule (with a few exceptions) remains united with one or two cells of the ventral wall of the adjacent saccule by means of a column of protoplasm, in the formation of which both or all three cells (*w.*, fig. 18) take part. Owing to the excess of nuclei in the ventral wall of the saccule we often find a column provided with two nuclei at its dorsal and one at its ventral end (*y.*, fig. 18), while some of the cells of the ventral wall become simple plaster-cells unattached to a column (*z.*, fig. 18). Similar double nuclei and plaster-cells are rarely found in the dorsal wall of a saccule. This arrangement of the nuclei is retained through all subsequent stages up to the adult form, and was found in the adults of all other spiders examined.<sup>1</sup> I also found it in embryos of *Agelena labyrinthica*, and it is evidently general amongst Dipneumonous spiders.

The nuclei vary greatly in shape. Many are more or less depressed in the plane of the septa, becoming plano-convex or conical, the plane side facing the chitinous cuticula.

The cells of the ventral wall of the oldest saccule (*s.* 1) require special mention. These also form columns, which attach themselves to the body hypodermis, but the cells of the latter do not contribute to these structures. The nuclei of this saccule are often drawn out in a peculiar way into the thinnest part of the ventral columns (fig. 17). Locy, who describes these columns, considers them to be probably of a muscular nature, but there does not seem to me to be any reason for thinking that they are any more muscular than the columns of the septa. Their greater length is simply explained by the fact that each cell has to form a column, at

<sup>1</sup> The plaster-cells were first noticed by Berteaux ('89) in fully developed spider's lungs.

least as long as the two-celled columns of the septa, in order to allow sufficient space for the blood-corpuscles to pass between the ventral saccule and the outer hypodermis.

Two authors, Locy and Jaworowski, deal with the formation of the definite lung-septa from the embryonic epithelia. According to Locy ('86), whose account differs from mine, the nuclei, which are in parallel rows, become plano-convex and arrange themselves in pairs, the convex side of each nucleus in one row being exactly opposite that of an adjacent parallel row (i. e., of an adjacent epithelium). Ultimately the cells of each pair of nuclei, which thus face each other, come in contact and fuse together to form the columns. The cells of such a pair of rows constitute the two walls of a flat, hollow sac, a respiratory lamella (i. e., a septa). Blood has a free access to the lamellæ at their anterior attachments. (Locy's statement that a septa represents a hollow sac is, of course, incorrect. He apparently considers them attached at their anterior ends only.)

Jaworowski's account ('94, pp. 60-61), is more in agreement with mine. According to him the space between the two layers of nuclei of a septum is filled with protoplasm and the lacunæ appear between the cells, and are at first small and roundish, and later on large and elongate. Jaworowski evidently intends to imply that the columns are the remains of the protoplasm left between the lacunæ, and his fig. 12 illustrates this very clearly. Here two, or even three nuclei may be observed at one or both ends of a column at first, but later on this is rarely or never the case, only one nucleus being found at each end of the column (in agreement with Locy).

**The chitinous lining of the pulmonary saccules.**—Shortly before the appearance of the lacunæ the walls of the saccules appear to collapse, and on the surfaces of contact, where the cavity was situated, two chitinous membranes are secreted. These pass over into one another at their medial, lateral, and anterior edges, so as to form a flattened chitinous saccule within the epithelial saccule, and are further connected by

innumerable tiny chitinous rods, which are firmly soldered to each membrane and distributed over their entire inner surfaces (*s.* 1, figs. 17 and 18). The ante-chamber is also provided with a smooth cuticula (*cu.*, fig. 18), except in the dorsal growing part (*pulm. prol.*).

The walls of the chitinous saccules are lined on one (the basal) surface with a thin layer of protoplasm, which is, of course, the matrix, and although this layer may become very thin (as, for instance, in *Agelena labyrinthica*), it is always distinctly recognisable at this stage. Locy could not trace the protoplasm on the chitin away from the columns in *Agelena naevia*, while Jaworowski ('94) describes these columns as amœboid in shape, sending out processes over the surface of the chitin to connect with those of neighbouring cells of the same epithelium.

**The moulting of the lung-books.**—It is well known that at each moult of the young spider the entire chitinous lining of both the ante-chamber and saccules is cast off (Menge, '51, p. 22; W. Wagner, '88, p. 315), and that the ventral walls of the latter produce the innumerable free spines on the surface of the cuticula (W. Wagner, '88, p. 314). Various points of interest still remain to be described in connection with the growth at moulting.<sup>1</sup>

Already at the time of hatching we find the saccules preparing for the first post-embryonic moult, although the latter does not take place until nearly a week later. The epithelia of each saccule expands in a medial, as well as in an anterior direction, considerably beyond the corresponding edges of its primitive chitinous lining, while the lateral and posterior edges remain stationary. The enlarged sacculus thus created then secretes over its interior surface a new cuticula forming a second chitinous saccule (*s'*., fig. 34), which encloses the one first formed (*s.*) and differs from it in structure. For its ventral membrane bears over that part of its area which is co-extensive with the primitive cuticular saccule (*s.*) nume-

<sup>1</sup> The following remarks on this subject apply equally to *Attus floricola*, *Agelena labyrinthica*, and *Tegenaria atrica*.



rous short cones (*c.*), not attached to the dorsal membrane, while in the newly added medial portion (*s'*.) the rods are fused with both membranes.

Herein lies the explanation of the greater thickness of, and the larger number of cells in, the ventral wall of the saccules in the earlier stages (fig. 13B) described on p. 29; for we may assume that the ventral wall secretes the numerous minute rods as well as the ventral cuticula of the primary chitinous saccules, and that only their dorsal cuticula is contributed by the dorsal wall of the saccules. Being in contact at first the rods of the ventral cuticula are able to fuse with the dorsal cuticula, but at the first moult and all subsequent moults the two cuticulas are separated by the previously formed chitinous saccule except along the newly added medial and anterior portions. The chitinous saccules first formed are cast off at the first moult, but they previously become squeezed very thin and are thus difficult to recognise as such.

At each subsequent moult the saccules are enlarged in the way described for the first moult, and since in the medial and in the anterior portion of the chitinous saccules at any period of life the rods are found soldered to both membranes, I conclude, generally, that this soldered region represents the portion that was added at the previous moult.<sup>1</sup>

My account of the primary chitinous saccules differs from that of both Locy and Jaworowski. The first-named author ('86) describes and figures the dorsal chitinous membrane of each saccule as smooth and the ventral membrane as denticigerous, but not united to the dorsal one in the embryo in *Agelena nævia*. In my sections of the embryos of *Agelena labyrinthica* the two membranes of the primitive saccules are undoubtedly fused together, exactly as in *Attus floricola*. According to Jaworowski's description, in the

<sup>1</sup> The same appears to be the case in many other spiders, although it has hitherto escaped the notice of investigators: so, *Argyroneta*, *Drassodes*, *Lycosa*, *Philodromus*, etc. There is no special reason why the added region should never have free rods, hence the above statement must not be applied too strictly to all spiders.

embryos of *Trochosa singoriensis* both the membranes bear granules (i. e. the teeth), and from his figures it is clear that these membranes are not fused together.

Both these authors' accounts may very easily be reconciled with one another and with mine, if we assume that their figures represent stages in which the preparation for the first post-embryonic moult had already begun. Locy's figures then would represent sections in which the new cuticula of the dorsal wall of the sacculus had separated from the primary chitinous sacculus and so appeared smooth, while the ventral cuticula would still appear denticerous. It may happen in *Attus floricola* that the ventral wall of the secondary chitinous sacculus ( $s'$ .) becomes pulled apart from the primary sacculus ( $s$ .), which, adhering to the dorsal wall, causes it to appear as if both walls of the sacculus were provided with denticles. This, no doubt, is the explanation of Jaworowski's statement.

**The operculum of the lung-books.**—It is well known from the observations of Morin ('87), Kishinouye ('90) and others that the outer epithelium of the pulmonary appendage forms the operculum, which covers each lung-book after the appendage has sunk into the body.

It will be observed from a comparison between figs. 13B and 17, and between figs. 16A or 16B and 18, that the sides, as well as the distal wall, of the abdominal appendage contribute to the formation of the operculum. Thus, in fig. 17 the ventral portion,  $w'.x'$ ., of the operculum, to which the ventral columns of the oldest sacculus,  $s.1$ ., are attached, correspond to the ventral wall,  $w'.x'$ ., of the appendage in fig. 13B, while the distal and dorsal walls,  $x'.y'$ . and  $y'.z'$ ., of the latter correspond as nearly as possible to the portions  $x'.y'$ . and  $y'.z'$ . of the operculum in fig. 17 (both figures being magnified the same number of times). A line (*pr. ax.*) through the centre of the area  $x'.y'$ ., or, say roughly, of the entire operculum, and perpendicular to its surface would, I think, correspond approximately with the original axis of the appendage.

Since the positions of the septa and the operculum remain



practically unchanged after the stage represented in fig. 17, we can distinguish in the operculum of the adult spider (1) a nearly horizontal portion to which the ventral saccule is attached, and which belongs to the ventral surface of the abdomen, and (2) a strongly inclined portion on the lower part of the lateral surface of the abdomen. The horizontal part corresponds to the ventral wall of the embryonic appendage in fig. 3 ( $w'.x'$  in figs. 13B and 17), or the median wall of an earlier stage (fig. 1), while the inclined portion, which forms much the greater part, is the distal and dorsal wall of the appendage, i. e.—the part  $x'.z'$  in figs. 13B and 17, or the distal and lateral wall of an early stage (fig. 1). Anteriorly the operculum curves strongly towards the median line, and this incurved part corresponds, of course, to the anterior wall of the embryonic appendage (fig. 18). All the surfaces pass over gradually into one another and cannot be sharply distinguished.

**The lung-books of the young spider.**—Not much remains to be added on the subsequent development.

At the time of hatching the lung-book has much the appearance of fig. 18, except that the pulmonary sac (now the ante-chamber) has much thinner walls, lined with chitin internally, and the dorsal saccules are longer. Moreover, that portion of the epithelium of the pulmonary sac immediately adjoining the spiracle now forms a thin-walled, narrow, hollow neck or stalk (pedicel) connecting the ante-chamber proper with the edge of the spiracle.

This pedicel persists throughout all later stages, and its chitinous lining acts both as an air-passage to the ante-chamber and as a sort of ligament by means of which the lung-complex is firmly attached to the outer cuticula of the body.

The dorsal horn of the ante-chamber preserves its characteristic curved form, and, as Bertkau ('72) showed long ago, continues to provide new lung-septa. According to W. Wagner ('88), the addition of new septa goes on until the age of sexual maturity is reached. In *Attus floricola* at the

time of hatching there are about seven or eight developed saccules. At the time of the second moult there are perhaps twelve to fourteen, while in the adult about thirty-four or thirty-five appear to be present, but I cannot state the exact numbers with certainty.

**Critical remarks on the literature.**—*Aranææ*.—According to Locy ('86, p. 81) the in-foldings for the lung-books in *Agelena nævia* arise late in the period of the reversion. From his figure (fig. 73) and description of "early stages" (p. 89), in which the lung-books appear as extensive groups of cells with the nuclei arranged in parallel rows, as well as from the fact that he makes no mention of any connection with the abdominal appendages, it is clear that Locy was really dealing with late stages after the appendage had already sunk into the body and long after the earlier saccules had been formed. Of the formation of these latter he gives no account. His account of the formation of the definite septa has already been dealt with on a previous page (p. 31).

Bruce's ('86a, '86b, '87) statements may be dismissed as disproved by later researches. Both Kishinonye ('90) and Simmons ('94) are of opinion that Bruce ('87) has misinterpreted the parts in his figures lxxix and lxxix'. Certainly the fold *L'* is not a pulmonary fold, and is not on the anterior surface of the first abdominal appendage, as Bruce supposes it to be.

Simmons ('94) states that the pulmonary sac arises as an in-pushing behind and under the abdominal appendage, "so that eventually a pit is formed, actually extending into the general body surface." The pit is considered as bounded on its outer side by the appendage itself, its outer wall being described as "the morphologically posterior surface of the appendage" (p. 217), which is represented as lying flat on the body surface and directed backwards. The opening of the pit under the posterior or distal end of the appendage persists as the spiracle. The outer wall of the pit "has its ectoderm thrown into folds, the rudiments of the leaves of the lung-book," and sections of early stages are figured, one

section (fig. 6) showing five pulmonary furrows and the other (fig. 5), although of the same age, only two such furrows.

It is plain that the author considers that the earliest lung-leaves are formed entirely within the pulmonary pit or sac and not on any part of the free surface of the appendage outside of the sac; so that, as far as the position of the lung-leaves in regard to the appendage at their first appearance is concerned, the author has not advanced beyond what was known to his predecessors. Nevertheless, in the summary at the end of the paper we find the following statement, that "the lung-book of the spider (and presumably of all Arachnids which possess one) arises at first as an external structure upon the posterior surface of the abdominal appendages" (p. 219).

If we accept the theory that the lung-books are derived from gill-books as indisputable, then we can say that the appearance of the lung-leaves on the outer or anterior wall of the pulmonary sac proves that this wall is morphologically the posterior side of the abdominal appendage, but we cannot conversely first call this wall the posterior side of the appendage and then say that the appearance of the lung-leaves upon it proves that they are formed on the posterior side of the appendage, as Simmons does. For if we choose to consider that the lung-books were derived from internal tracheæ and not from external gill-books, the pulmonary sac would be the trunk of a trachea, and no one would then call its outer wall the posterior wall of the appendage. Thus, if Simmons' description of the early development were correct, then the lung-books would not arise at first as an external structure, but as an internal one in an invagination.

As a matter of fact Simmons' representations of the abdominal appendage in his figs. 5 and 6 are very misleading, as will appear if we refer to his fig. 10, which represents an entire embryo of the same age as those in figs. 5 and 6. Here the first abdominal appendage has its usual stumpy, knob-like form, and is situated on opposite sides of the abdomen, almost antipodal in fact, just as in *Attus floricola*.

Sagittal sections, like Simmons' figs. 5 and 6, therefore, cut the appendage more or less transversely to its main axis, which in the two figures would be, not in the plane of the paper, but almost perpendicular to it.

In fact I cannot believe that the appearance of the appendage in *Agelena naevia* at this stage differs so essentially from the corresponding stage in *Attus floricola*, such as that represented by my fig. 16. A sagittal section in the case of the appendage represented in this figure would, of course, be more or less perpendicular to the plane of the paper and cut the appendage parallel to the line *ep.-ep.* If the section were slightly more inclined towards the lower part of the paper (say along *a.-b.*, fig. 16B) we should get a section like fig. 15, but if it were inclined more towards the upper part of the paper (say along *c.-d.*, fig. 16B), we should get sections exactly resembling Simmons' figs. 5 and 6, according as two or five of the furrows were cut. This I believe to be the true explanation of the appearance of Simmons' figures. It is extremely difficult, if not impossible, to get an exact idea of the structure of an appendage without the aid of wax models, of which Simmons does not say he made any use.

The last paper on the spider's lung-book to be considered is that of Jaworowski ('94), who studied *Trochosa singoriensis*. He discovered in this species an embryonic structure, which he describes as an embryonic trachea, consisting of an ante-chamber, a trunk, and branches. The ante-chamber is inverted funnel-shaped, with the apex pointing upwards and the broad end terminated ventrally by the abdominal appendage or operculum. The sides of the ante-chamber are closely appressed to one another (p. 56) and extended in a sagittal plane (since they are seen broadways in sagittal sections). The pulmonary lamellæ are formed by parallel folds of the wall of the ante-chamber, "the edges of the folds, which jut into the lumen, being more or less (figs. 1 and 2) undulate" (p. 62) and parallel to the surface of the operculum, i. e., transverse to the axis of the ante-chamber and trachea.

According to Jaworowski's idea, therefore, the free edges

of the septa run parallel to the longitudinal axis of the abdomen instead of at right angles to it, as they do in *Attus floricola*, etc. Now if we compare my figs. 13B and 17 of transverse sections with Jaworowski's figs. 3 and 5,<sup>1</sup> which come just in between mine in point of development, it will be seen that the lung-books of both species exactly correspond, so that the free edges of the septa cannot run longitudinally to the body axis. In fact, Jaworowski has evidently mistaken the direction of the folds, which are seen laterally in his figs. 3 and 5 and not from their free edges; and, moreover, the funnel-shaped area which he calls the ante-chamber in his sagittal sections is not the ante-chamber at all.

The trunk of the embryonic trachea, according to Jaworowski, extends dorsad from the apex of the ante-chamber and then divides, the branches reaching to the dorsal blood-vessel and subdividing into smaller branchlets. These have sometimes the appearance of a cuticular tube provided with regular internal thickenings (fig. 6). Ultimately both trunk and branches degenerate and disappear, only the "ante-chamber" remaining to form the lung-book.

In the later stages of the spider-embryos which I examined, I find the yolk-mass continuous along the median region but divided towards the sides by partial septa, which are transverse and doubtless of mesodermal origin. The surfaces of the yolk are lined with very thin flat cells, and the intra-septal space between these two layers of cells contains muscles, blood-corpuseles, and a number of large vitellophagous cells resembling those marked *vit.* in my figs. 16D, 16E, 17, etc. Ventrally the intra-septal spaces widen out, the widened part appearing funnel-like in sagittal sections (see fig. 41, which shows three such septa). The lung-books lie in the ventral widening of the septum between the eighth and ninth segments. The space between the lung-books and the

<sup>1</sup> The author calls these "frontal sections," but since the abdomen is inclined ventrally to the longitudinal axis of the cephalothorax, frontal sections of the latter would cut the abdomen more transversely than frontally. (See Locy's fig. 10 or Korschelt and Heider, p. 585, fig. 372B.)



yolk also contains blood-corpuscles, vitellophagous cells, and various mesodermal elements, besides fluid.

Jaworowski's tracheal trunk and ante-chamber undoubtedly correspond in position to the lower part of the septum and its funnel-shaped widening, but I have found nothing in them in my sections which could possibly be taken for tracheæ. Jaworowski states that the trunk has a nucleated epithelium, the nuclei being smaller than those of the pulmonary lamellæ (p. 62). These may well be, I think, the nuclei of the mesodermal septa, but I am at a loss to account for the tracheal branches and branchlets drawn by Jaworowski in his figs. 1 and 2. At any rate the tracheal nature of the structure cannot possibly be maintained so long as no embryological evidence at all is advanced to prove that they are of ectodermal origin and derived from the same mass of cells which form the lung-books. It will be noticed further that the lumen of the ante-chamber is closed off from that of the tracheal trunk by a diaphragm (p. 63).

No other investigator has ever found anything like these embryonic tracheæ, and although Jaworowski ('94, p. 55) asserted that Schimkewitsch ('86a, '86b) had previously observed a similar structure, the latter author has recently (:06, p. 45) disclaimed any connection between that figured by him and those found by Jaworowski.

Scorpiones.—Metschnikoff ('71), Laurie ('90 and '92), Brauer ('95) and Pereyaslawzewa (:07) all agree that the lung-books of scorpions arise as folds in the wall of the pulmonary sac, which according to the first three authors is formed by invagination on the posterior sides of the four posterior pairs of abdominal appendages. According to Pereyaslawzewa, however, this sac arises on the anterior side of the appendages, but it appears to me probable that this author has mistaken the intersegmental folds which separate the sternites for appendages, the true appendages described by previous authors having evidently already disappeared.

Brauer states that, so far as he could make out, the oldest pulmonary fold occurs at the innermost part of the sac, the



following folds occurring on the distal side of this one (i. e. exactly opposite to what takes place in spiders). The author does not appear to be quite certain about this point, and is, moreover, corrected by Pereyaslawzewa, who maintains that the oldest fold is the one nearest to the outer body wall (i. e. as in spiders).

Brauer's text-fig. 15c (p. 413) very closely resembles my fig. 16b, so far as the ectoderm is concerned. He thinks there can be scarcely a doubt that the lung-book is not formed behind or apart from the appendage, but is the posterior half of the latter itself, which is invaginated and on which the pulmonary folds appear (p. 415).

Laurie ('92) makes an interesting statement regarding the position of the lung-septa in the older scorpion-embryos, Here they are placed horizontally, as in the older spider-embryos, whereas in the adult scorpion they are vertical (p. 102).

Pedipalpi.—The development of the lung-sacculæ and their relation to the abdominal appendages do not appear to me sufficiently clear, from the existing embryological data, to make a comparison with the Araneæ possible. Apparently the abdominal appendages are not so obvious in this group as they are in Araneæ and Scorpiones, since the parts described by Laurie ('94) under this name are not identical with those to which Schinkewitsch (:06) applies the term.

A remarkable point in the development, as described by Schinkewitsch, is that the oldest sacculæ are said to be formed within the pulmonary sac and to subsequently migrate out of it on to the posterior side of the appendage. In such a case their development would be exactly the opposite to that in Araneæ, as well as to what we should expect from phylogenetic considerations.

Pereyaslawzewa's (:01) description of the formation of the lung-septa out of the cuticular wrinkles of the body-surface is altogether fanciful.

**The fully-developed lung-books of spiders.**—A. Schneider ('92) has given an excellent account of the coarser anatomy of the

lung-books in spiders, the descriptions of MacLeod ('84) and Berteaux ('89) being unsatisfactory in this respect. Berteaux's account of the chitinous structures (spines, etc.) of the lung-books is, however, very detailed and the best we possess, but his description of the bi-nucleated cell-columns in the septa as unicellular structures is misleading and not in accordance with the embryological facts, since these columns are formed by the fusion of opposed cells in two separate epithelia.

Both MacLeod and Berteaux made a curious error regarding the free edges of the septa. The edges of the septa they describe as being free, not only along the posterior border but along the posterior part of the lateral side as well. As a matter of fact the lateral sides of the septa are never free, but may have the appearance of being so in horizontal sections through the dorsal procurved portion of the antechamber. The apparently free edge is merely that of a septum with its lateral part cut off by the razor, hence the irregularities in its occurrence observed by these authors. That these lateral edges are not free can easily be demonstrated by examining the lung-books under a hand-lens after treatment with caustic potash, and I can strongly recommend this old-fashioned method to anyone who wishes to obtain a clear idea of the coarser structure of the lung-books in a short time (see fig. 20). It will be found much more satisfactory than if one were to rely on sections only.

Börner (:04) has recently stated that the septa are placed more or less vertically in the majority of the Araneæ, and has thrown doubt on MacLeod's well-known diagrams, in which the septa are represented as lying horizontally.

I have examined one or two species of most of the larger families and I found the septa as nearly horizontal as they could well be in the following Dipneumonous spiders: Attidæ (*Attus floricola*), Lycosidæ (*Lycosa Darlingi*), Agelenidæ (*Tegenaria domestica*, *Textrix lycosina*), Clubionidæ (*Clubiona holosericea*, *Palystes* sp.), Thomisidæ (*Philodromus fuscomarginatus*), Theridiidæ (*Theridion lineatum*), Drassidæ

(*Drassodes tessellatus*), Sicariidæ (*Scytodes tessudo*); also in the following Tetrapneumonous spiders (Aviculariidæ): subfam. Aviculariinae (*Harpactira atra*), subfam. Ctenizinae (*Stasimopus unispinosus* and *Hermacha* sp.).

In the following forms the septa were inclined at an angle of  $45^{\circ}$  or less to the horizontal, sloping downwards from the higher medial edges to the lower lateral edges: Argiopidæ, subfam. Argiopinae (*Argiope clathrata*), Theridiidæ (*Latrodectus geometricus*), and Eresidæ (*Eresus* sp.).

If the above examples are any indication of the usual position in the families to which they belong, then Börner's statement must be wrong, and cannot hold good for the great majority of Araneæ. Even in the three cases where the septa were inclined they were nearer the horizontal than the vertical (except, perhaps, in *Latrodectus geometricus*, where they formed an angle of about  $45^{\circ}$ ).

Moreover, the operculum in the spiders with horizontal septa is similar to that of *Attus floricola* described on p. 49 (see fig. 17), and since this type of operculum represents that of any Dipneumonous or Tetrapneumonous spider in which the abdomen is not greatly developed anteriorly, we may fairly assume that the septa must be horizontal, or very nearly so in the great majority of spiders.

When, however, the anterior upper region of the abdomen is abnormally distended above the opercula, it may happen that the lateral region of the latter becomes pushed downwards into a more horizontal position than is the case in fig. 17, and at the same time the septa become tilted upwards on the medial side, that is to say, they take a more or less inclined position, such as one finds in *Argiope*, *Latrodectus*, and *Eresus*, and no doubt in many other genera of the same families. The inclined position of the septa cannot, therefore, be a primitive condition in these families, but, I think, merely due to the abnormal distension of the abdomen, for in closely allied forms, in which the abdomen is not

unusually distended and the operculum more upright, I find the septa placed almost horizontally (e. g. in a specimen of *Nephila* from Senegal).

## VI. THE DEVELOPMENT OF THE ABDOMINAL LONGITUDINAL MUSCLES AND THEIR TENDONS.

In their earliest stage the coelomic sacs of the eighth to eleventh segments each protrude an evaginated portion of their somatic wall into a provisional appendage, completely lining the cavity of the latter (fig. 4). At this stage (*St.* 1) the cells of the somatic wall of the sac are cylindrical, and much higher than those of the splanchnic wall.

At the time when the first pulmonary furrows begin to appear (stage 2) the intra-appendicular portion becomes partially cut off from the main coelomic sac by an infolding of its wall along the medial basal edge of the appendage (fig. 1). The infolded layer grows in a lateral direction halfway across the cavity of the appendage, converting the medial half of the intra-appendicular coelom into a short tube. Each of these segmental tubes lies in a transverse plane, is blind at the medial end, and opens laterally into the coelomic sac.<sup>1</sup>

In a longitudinal section through the lateral region of the appendages (*ab. app.* 1-3, fig. 5A) the main coelomic cavity is seen to be continuous with the intra-appendicular portion, whereas the latter portion in a more medial section of the same series (fig. 5) appears separated from the main coelom, the segmental tubes (*seg. t.* 8-10), of course, being seen in cross section. If this latter section be compared with a corresponding section of a later stage (fig. 6, stage with five pulmonary furrows), it will be noticed that the portion of the somatopleura which formed the inner layer of the above-

<sup>1</sup> I have shown elsewhere ('95) that the segmental tubes of the eighth or pulmonary segment become the genital ducts. In fig. 23B (adult male) the mesodermal part of the genital duct (*mes. g. d.*), derived from the segmental tubes, is seen sharply differentiated from the ectodermal portion (*ec. g. d.*).

mentioned fold, and which overlies the segmental tube, has increased considerably in thickness in each segment. Its cells (*m.*, fig. 6) are no longer cubical and one-layered, as they are in fig. 5, but have become spindle-shaped, elongated longitudinally to the body, and arranged in several layers. Each such group of elongated cells forms a bundle whose ends are in contact with the anterior and posterior basal edges of the appendages, thus completely bridging over the segmental tubes, and ultimately gives rise to a corresponding segment of one of the two great ventral longitudinal muscles of the abdomen.

The ectodermal areas to which these muscular segments are attached are of primary importance in enabling us to determine the homologies of the tracheæ. In their earlier stages it will be seen that these areas (*ar.* 7-11, figs. 6 and 27) are precisely similar to each other in position and arrangement with regard to each appendage. They occupy the visceral surface of the medial half of each post-appendicular (intersegmental) in-folding,<sup>1</sup> and their transverse extension is at first nearly the same as that of the segmental tubes with which the areas alternate.

Each contact area soon becomes marked by the appearance of the intermuscular tendons or entochondrites. These organs, whose mesodermal origin has already been demonstrated by Schimkewitsch ('94) are formed in various parts of the body by the fusion and metamorphosis of the ends of the muscular cells at those places where the ends of two or more muscle-bundles come in contact with each other and with the hypodermis.<sup>2</sup> In the embryo they form a non-

<sup>1</sup> For the area (*ar.* 7) between segments 7 and 8 there is, of course, no post-appendicular in-folding, but its position is otherwise precisely similar to that of the others.

<sup>2</sup> Schimkewitsch, to whom we mainly owe our knowledge of the development of the entochondrites in Arachnida, has a somewhat different view of the conditions necessary for the formation of these organs. He says ('94, p. 206): "Mann kann behaupten, dass in jenen Fällen, wenn zwei Muskelanlagen einander entgegen wachsen, sie mit einander verwachsen; wenn sie aber unter einem Winkel zusammen-

nucleated homogeneous mass, which stains very deeply with carmine, and is, histologically, readily distinguishable from all adjacent tissues. All the cells of the ventral longitudinal muscles become subsequently attached by each end to these entochondrites only, which in turn firmly adhere to the bases of the ectodermal cells of the deepest part of the contact-area described above, and provide us with a certain means of locating these latter cells long after the subsidence of the appendages. It should be noted that the entochondrites are much less extensive at first than the ectodermal areas (*ar.* 7, etc., figs. 6 and 27) with which the ends of the forming muscles were originally in contact.

From what has just been said, there can be no doubt that the places of attachment of the entochondrites inserted in each ventral longitudinal muscle are serially homologous, a fact which may also be readily inferred from a glance at fig. 41, which represents the stage shortly before hatching. From this figure it may also be observed that several other muscles are attached to the entochondrites (*t.* 7-11), in addition to the segments (*v. l. m.* 7-11) of the great longitudinal muscles as, for instance, (1) a long dorso-ventral muscle (*d. v. m.* 7-10); (2) a short, oblique muscle (*p. ob. m.* 8-11) running obliquely forwards and attached near the middle of its segment to the hypodermis without the interposition of an entochondrite; and (3) a corresponding oblique muscle<sup>1</sup> (*a. ob. m.* 8 and 10), running obliquely backwards, present in segments 8 and 10. In *Agelena labyrinthica* I also

treffen, so bildet sich an der Stelle ihrer Berührung eine Sehne mesodermalen Ursprungs." To my mind it does not matter whether the muscles are in a line or meet at an angle, the essential conditions being only that the ends of two or more muscles should meet at one spot and that that spot should be on the basal surface of the hypodermis. When muscles are attached singly to the hypodermis they do so directly without the intervention of an entochondrite.

<sup>1</sup> I have called this muscle-series and that previously mentioned the anterior (*a. ob. m.*) and posterior oblique muscles (*p. ob. m.*), because they lie in the anterior and posterior regions respectively of their somites.



found an oblique muscle on the medial side of the entapophysis of the pulmonary segment, which, perhaps, corresponds to a muscle (*a. ob. m. 9*) not observed in *Attus floricola*.

In the embryo and the growing spider the ectodermal areas to which the entochondrites of the longitudinal muscles are attached become drawn out in the form of hollow processes (*ec. t. 8-11*, fig. 41), lined with chitin, and projecting into the interior of the body. These are the ectodermal tendons or entapophyses<sup>1</sup> (apodemes) of the ventral longitudinal muscles, and it was the purpose of the foregoing paragraphs to establish their serial homology.

Since the segments of the longitudinal muscles are each formed out of the entire length of the somatic wall of a cœlomic sac, it follows that their points of attachment (or the entapophyses) must be intersegmental, and this is also the case with the points of attachment of the dorso-ventral muscles where they coincide with those of the longitudinal muscles (as, for instance, the ventral end of the muscle *d. v. m. 8*, and both ends of *d. v. m. 9* and *10* in fig. 41). But it frequently happens in the Arachnida that the dorso-ventral muscles disassociate themselves at one or both ends from the insertions of the longitudinal muscles, and may then form separate external depressions, which are not necessarily intersegmental, but, in fact, very frequently placed more forwards on the face of the segment. Thus in fig. 41 the muscle *d. v. m. 8*, although actually in contact at the place of crossing with the dorsal longitudinal muscle (*d. l. m. 8*) of the eighth somite, is inserted dorsally at some distance in front of the intersegmental entochondrite which lies between the muscles *d. l. m. 8* and *9*.

#### VII. THE ENTAPOPHYSES (ECTODERMAL TENDONS) OF THE PULMONARY SEGMENT.

When the entochondrites begin to form at about the stage with five pulmonary furrows, the first pair of provisional appen-

<sup>1</sup> A term introduced by Ray Lankester.

dages has reached its most lateral position (fig. 3). The anterior wall of appendage 2 has approached nearer to appendage 1, so that the ectodermal area (*ar.* 8, figs. 6 and 16), to which the entochondrite becomes attached, now forms the bottom of a rather wide groove lying between the two appendages towards their medial side. Shortly afterwards the three posterior provisional appendages commence to move towards the posterior ventral part of the abdomen away from appendage 1.

Now, as the latter retains its lateral position for the present and is very close to appendage 2, we find the area (*ar.* 8) between them, to which the tendon is attached, also shifting slightly ventrad. In fig. 27 the appendages are still in a row, but the ventrad movement is commencing; in fig. 16 (a slightly later stage) appendage 2 has moved ventrad to the region comprised between the sections nos. 1-18, and the area of attachment (*ar.* 8) is no longer just behind the region of the two oldest furrows (*f.* 1 and *f.* 2), as it appears to be in fig. 27, but lies ventrally to them. When this area has reached the extreme postero-ventral corner of the base of the appendage, it remains there, while appendage 2 continues its ventrad movement.

The subsequent development up till after the second moult is a simple one. After the completion of the reversion and shortly before hatching (stage 6) we find the entochondrite (*t.* 8, fig. 41) situated alongside the posterior median corner of the lung-complex (*lb.*), just next to the medial end of the spiracle. The ectodermal area (*ec. t.* 8) to which the entochondrite is attached, is composed of elongated cells and is somewhat sunken-in, forming a shallow, groove-like continuation of the spiracle (*sp.*, fig. 18). At the second moult, when the young spider attains its definite form, this groove becomes obliterated, so that the hypodermis of the attachment area comes to lie on a level with the adjacent body surface and completely outside of the spiracle.<sup>1</sup>

<sup>1</sup> In *Agelena labyrinthica* the groove is present in all stages after the time of hatching.

As the young spider, however, approaches maturity, the attachment area again undergoes a considerable alteration in its form and position, resulting mainly from two processes. These consist in (1) the formation of a transverse in-folding of the hypodermis (the interpulmonary fold) between the two spiracles, which thus become connected by a deep ventral groove; and (2) the drawing-out in the form of a blind tube (entapophysis) of the dorsal edge of this fold at the two spots to which the pair of mesodermal entochondrites are attached.

**The interpulmonary (epigastric) fold in the adult of *Attus*.—**Fig. 20 represents a posterior view of the abdominal chitinous skeleton of an adult of a species of *Attus*, after the removal of everything posterior to the transverse plane which passes through the spiracles. It will serve to illustrate the form of the interpulmonary fold in the adult.

In *Attus floricola* the interpulmonary fold in the male differs greatly from that of the female.

Figs. 23-23B are three sagittal sections through this fold in the adult male in the regions indicated in fig. 20. The much crumpled, anterior and posterior surfaces of the groove contained in the fold are normally closely applied to each other, so as to leave very little space between them. Along the dorsal edge, however, this is not the case, for here the groove suddenly widens to a nearly cylindrical canal (*can.*), which opens on each side into the pulmonary ante-chambers at their medio-ventral corners, thus forming a permanently open communication between the two lungs ["canal of communication" observed by Berteaux ('89) in *Agelena* and *Epeira*]. The chitinous wall of the canal is thick and covered with branched anastomosing spines, quite similar to and directly continuous with those of the ante-chambers.

The two entapophyses (*ec. t.* 8) have each the form of a short, strongly compressed pouch, whose blind end is directed upwards, backwards and laterad. The cavity in the ventral part of each branches off from the interpulmonary canal, and is provided, like the latter, with anastomosing

spines (*spi.*, fig. 23A), while near its blind dorsal end it is without any spines (*cc. t. 8*, fig. 23A).

The hypodermis of the blind end is of special interest. Its cells assume a fibrous structure (*hy'*, fig. 23) and are not pigmented like the adjacent hypodermis, and the large entochondrite (*t. 8*) is firmly attached to their basal ends.

The numerous and powerful muscles which are attached to this entochondrite have been described by Schimkewitsch ('84), Vogt ('89), A. Schneider ('92), and others. It corresponds to the anterior of the three pairs of abdominal entochondrites described by these authors.

In females of *Attus floricola*, at any rate in matured or nearly matured specimens, the interpulmonary fold differs in a very remarkable manner from that just described. Instead of the cylindrical spinous canal of communication one finds a broad, thin-walled, much wrinkled, band-shaped canal, without spines internally, and strongly compressed from before and behind (*can.*, fig. 22). Moreover, the two walls of the fold itself, apart from the canal, are much more strongly wrinkled than is the case in the male.

In the adults of both sexes the opening of the genital organs is found on the anterior wall of the medial region of the fold between the pair of entapophyses (*g. o.*, figs. 20 and 23E).

**The interpulmonary fold in other spiders.**—The interpulmonary fold<sup>1</sup> was found in all Dipneumonous spiders examined by me, and in the majority of the genera resembled the conditions occurring in either the male or the female of *Attus floricola* (*Marpissa* ♂ ♀, *Clubiona* ♀, *Agelena* ♀, *Pisaura* ♀, *Dolomedes* ♀, *Melanophora* ♂ ♀, *Drassodes* ♀, *Zora* ♀, *Linyphia* ♀, etc.).

The pair of entapophyses are very variable in shape, even in the same species; thus out of five specimens of *Tegenaria domestica* (fig. 21) examined, no two had the entapophyses shaped exactly alike. In some forms these tendons may be

<sup>1</sup> This fold was known to Treviranus ('12), and is described by MacLeod ('84), Berteaux ('89) and others.

far apart (*Attus* sp., fig. 20), in others, again, close together (*Tegenaria domestica*, fig. 21), or even fused to a single, rounded, median lobe (*Lycosa Darlingi*). The free end or ends are either sub-entire or else drawn out into short finger-like processes (fig. 21). Except in the *Dysderidæ* the entapophyses are more or less inclined backwards.

The interpulmonary canal varies considerably, and is frequently spined and even cylindrical in the female as well. In the majority of cases it forms a canal of direct communication between the ante-chambers of the pair of lung-books, as in *Attus floricola*, but in the *Lycosidæ* and in *Phlodromus* this is not the case, the interpulmonary fold being rudimentary in the lateral part between the entapophysis and the lung-book. In many *Lycosidæ* this portion of the fold is represented merely by a slight internal thickening of the cuticula (*interp. fld.*, fig. 19A), but in *Phlodromus* there is a slight in-folding of the outer surface as well (fig. 19B) without an actual lumen being formed. The presence of these rudiments indicates that there was once a well-developed fold connecting the pulmonary sacs with the entapophyses, and that the present condition is a secondary one.

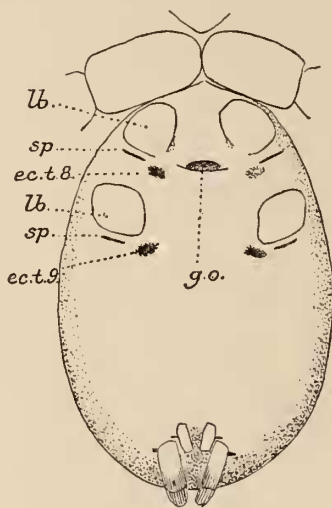
In *Argyroneta* (♂) the fold is well developed throughout, but there is no canal of communication, the two surfaces of the fold being closely apposed and without a lumen between them (fig. 19c).

In the *Dysderidæ*, too, there is no spinous canal of communication, although in the median part the lumen may be widened (*interp. fld.*, fig. 40). In *Dysdera* and *Segestria* the fold is deep and well developed between the pair of entapophyses, but on the lateral side of these it is rudimentary and not continuous with the spiracle. In *Harpactes* the fold is much less deep than in the two other genera, and the entapophyses are hardly specially distinguishable at all, being merely slightly deeper portions of the fold, to which the entochondrites are attached. The lateral portion of the fold is, how-

ever, here directly continuous with the spiracles. The male (but not the female) of *Harpactes* is also remarkable in that the opening of the genital organs lies immediately in front of, but separate from, the interpulmonary fold (*g. o.*, fig. 40), whereas in all other Dipneumonous spiders examined the genital opening lies in the anterior wall of the fold.

In the Tetrapneumonous spider<sup>1</sup> examined I found no inter-

TEXT-FIG. 2.



2.

*Crypsidromus intermedius*. Ventral surface of abdomen.  
*lb.*, opercula of lung-books; *sp.*, spiracles of lung-books;  
*ec. t. 8* and *9.*, muscle insertions; *g. o.*, genital opening.  
 Magnified 6.

pulmonary fold connecting the spiracles, but on the medial side of the latter (but separate from them and from the genital cleft) shallow depressions resembling stigmata in the cuticula were observed (*ec. t. 8* and *9*, text-fig. 2), which proved in sections to be the places to which the entochondrites of the ventral longitudinal muscles are attached. These rudimentary

<sup>1</sup> Specimens labelled "*Crypsidromus intermedius*, Paraguay," obtained from the Berlin Zoological Laboratory.



entapophyses (*ec. t.* 8, fig. 36) were similar in both pulmonary segments.

The only other order possessing the interpulmonary folds is the Pedipalpi, in which these folds are very well developed in both pulmonary segments and much resembles that of Dipneumonous spiders (see Tarnani, '89 and :04, and Börner, :04).

#### VIII. THE DEVELOPMENT OF THE TRACHEÆ AND THE ENTAPOPHYSES OF THE TRACHEAL SEGMENT.

The tracheal appendages are, as nearly as possible, the exact counterparts of those of the pulmonary segment in the earliest stages, up to, say, the period when the pulmonary furrows begin to appear (compare *ab. app.* 1 and 2 in fig. 4). The post-appendicular groove (*gr.*) extends along the whole posterior side of the appendage (except, perhaps, as in appendage 1, at the extreme lateral part), but it does not appear to be deeper laterally than medially.

In the stage with two pulmonary furrows (figs. 1, 5 and 5A), however, after the simultaneous subsidence of the epithelium lying between consecutive abdominal appendages we find that the post-appendicular groove is not almost obliterated in its medial half (*tr. s.*, fig. 5), differing in this respect from the corresponding groove of the pulmonary segment (*gr.*, fig. 5). On the contrary the infolding containing the groove has increased in depth along its whole extent, and continues to deepen in the following stages in such a way that its blind bottom is directed slantingly forwards (*tr. s.*, fig. 6A). This in-folding is the tracheal sac.

If we examine a reconstruction of the appendage from the inner surface (fig. 27) at this stage (when about five pulmonary furrows are present and the mesodermal entochondrites begin to be formed), we find a broad transverse ridge (*tr. s.*) projecting into the body and nearly co-extensive with the posterior side of the base of the appendage. This ridge is the ectodermal in-folding which forms the tracheal sac. The

space (*ar.* 9) occupying the medial region of its visceral surface and enclosed by the dotted lines in the figure is the area with which the ends of the longitudinal muscles are in contact, and to the deepest part of which the entochondrite becomes attached. The medial area (*ar.* 9) of the tracheal sac is, therefore, serially homologous with the corresponding area (*ar.* 8) behind the pulmonary appendage (see p. 20), and has consequently nothing to do with the region in which the earlier pulmonary furrows appear, nor with any portion of the lung-books. It will be observed that owing to the presence of the lung-leaves the area (*ar.* 8) in the pulmonary segment is more widely separated from the segmental tube (*seg. t.* 8) than is the case in the tracheal segment.

The lateral region of the tracheal in-folding is of especial interest, as it is the only part which is serially homologous with the pulmonary sac. It will be remembered that the pulmonary sac proliferates in a lateral direction (position as in fig. 1), later in a dorsal direction (position as in fig. 3), in the form of a hollow tuber-like process creeping along the inner surface of the outer epithelium; and that this sac and its proliferations yield the cell-material for the formation of the fourth and following pulmonary saccules.

Now the tracheal post-appendicular in-folding begins to proliferate laterally simultaneously with the pulmonary sac in precisely the same manner and direction. But the walls of the tracheal sac have not to furnish cell material for lung-saccules, of which no traces are present at any time, and, no doubt, on this account the pulmonary sac rapidly outgrows the corresponding tracheal sac, and in the stage of fig. 27 already greatly exceeds it in size. In this figure the groove (*tr. l.*) behind the tracheal appendage extends dorsally up to section No. 16, while the proliferation extends through five more sections; and the groove (*pulm. l.*) behind the pulmonary appendage reaches to section No. 24, while the corresponding proliferation extends further likewise through five more sections.

Figs. 35-35A and 16D-16E represent longitudinal sections

through the tracheal and pulmonary proliferations respectively of one and the same embryo from a series of sections similar to those from which fig. 27 has been reconstructed and representing the same stage. It is to be noticed that the tracheal proliferation (*tr. prol.*) is solid throughout, while that of the pulmonary sac (*pulm. s.*) is provided with a considerable cavity, though this is, of course, not a fundamental difference but is to be considered rather as due to a mere difference in the rapidity of growth. In other respects both proliferations closely resemble each other: in each the incision between it and the outer epithelium is deepest on the anterior side and dorsally at the apex. The opening of the tracheal sac does not extend dorsally beyond section No. 16 (fig. 6A) of fig. 27, the following five sections (compare figs. 35 and 35A) showing no trace of a post-appendicular groove, exactly as in the case of the corresponding five sections (Nos. 25-29) of the pulmonary appendage. In both cases the dorsal ends of the openings represent the latero-dorsal ends of the permanent spiracles, the medial ends of which are still unformed.

Shortly after the stage I have just described the migration of the three posterior pairs of abdominal appendages, already alluded to on a previous page, commences. This process, which may be considered as characteristic of all Dipneumonous spiders with the tracheal spiracle near the hind end of the body, consists of a double movement, namely, a medio-ventrad movement of each of the three pairs of appendages and a caudad one caused by the enormous elongation of the ninth somite. Near the end of the reversion, as a result of this process, these appendages come together in pairs in the median line in the posterior half of the abdomen (*tr. pl.*, figs. 41 and 43). At the same time the tracheal appendages gradually sink to the level of the body surface.

During this period the formation of the tracheal spiracles is completed, the lateral ends of the spiracles having already been formed at an earlier stage. The unformed median ends become approximated by the migration of the appendages towards the median line, and subsequently the region of the

body-epithelium lying in between (*inf.*, fig. 28) folds into the body, and the two spiracles become united to a single one (*sp.*, fig. 28).

Meanwhile, important changes have taken place in the post-appendicular sac of the tracheal appendage. Fig. 28 represents a reconstruction seen from above of the ectoblast of the two tracheal sacs (together with four muscles and two entochondrites) at the end of the reversion. Fig. 41 is a sagittal, and fig. 43 a transverse section of the same stage. The right half of fig. 28 is equivalent to the tracheal in-folding (*tr. s.*) in fig. 27, dorsal in the latter figure corresponding, of course, to lateral in fig. 28.

We observe in the first place (fig. 41) the great longitudinal elongation of segment 9, bringing the tracheal spiracle (*sp.*) and sac nearer to the posterior end of the abdomen. As if to compensate for this backward migration the medial region of each tracheal in-folding, that is, the region corresponding to the area *ar. 9*, fig. 27, to which the entochondrite is attached, becomes drawn out in the form of an elongated plate (entapophysis, *ec. t. 9*, figs. 41 and 28), which is directed forwards and slantingly upwards and is much compressed dorso-ventrally.

The entochondrite (*t. 9*) is attached to the narrowed anterior end of the plate, and at the extreme posterior lateral corner of the latter a second entochondrite (*t.*, fig. 28) is found attached to those cells which bound the lateral angles of the spiracle. Between these two entochondrites the anterior oblique muscle (*a. ob. m. 10*) is stretched.

The bulging lateral portion (*tr. prol.*) of each plate corresponds to the dorsal proliferation of a previous stage (*tr. prol.*, fig. 27). In the line of the transverse section, fig. 43 (see fig. 28), the lateral edge of the plate (*tr. pl.*) is some little distance from the outer hypodermis (*hy.*) but more posteriorly, near the entochondrite *t.*, fig. 28, the edge of the plate comes nearly or actually into contact with the outer hypodermis.

The pair of plates are connected like the spiracle by the

in-folding (*inf.*, fig. 28) of the epithelium between them, and, therefore, possess a common lumen, which, however, is confined to the basal region only and denoted in the figures by the area, *tr. l.*, within the dotted lines. The greater part of each plate is, therefore, solid. Fig. 28 gives the correct outline of the pair of plates, as they appear near the end of the embryonic period, and I have tested the accuracy of the reconstruction by comparisons with sections cut parallel to the tracheal plates, so as to contain the whole width of the pair of plates in one section. I could not detect a distinct chitinous lining within the lumen of the plate at this stage, for the cuticula which previously covered the body surface always appeared quite loose and outside of the cavity, as if the embryo were undergoing a moult such as Locy describes for *Agelena*.

If the tracheal and pulmonary appendages be now compared, the difference in the relative development of the two main organs connected with them becomes apparent. The entapophysis is small in the pulmonary segment but large in the tracheal segment, where it forms the greater part of the tracheal plate, while the large mass of cells composing the lung-book is represented by the comparatively small, lateral, bulging portion of the tracheal plate.

**The post-embryonic development of the tracheal plate.**—After the hatching of the embryo very important changes take place in the shape of the tracheal plates. In the first place the medial tendinal portion of each becomes drawn out in a forward and upward direction to form an elongate, spathulate, hollow process, which is strongly flattened dorso-ventrally and much broader anteriorly than in the middle. Its shape may be seen in fig. 29, which gives an accurate representation of the pair of plates after the first post-embryonic moult (stage 8). The tracheal lumen (*tr. l.*) now extends to near the anterior end, where it is also broader, but since the dorsal and ventral surfaces are practically in contact (fig. 29A) this portion can scarcely function as a respiratory organ at this stage.

In the second place, the lateral tracheal proliferations (*tr. prol.*) have also considerably elongated, but in a lateral direction to form a broad flattened lobe on each side. A portion of the lumen of the trachea is continued into the basal part of this lobe, and I have indicated the lumen by the dotted lines (*tr. l.*), as far as I could trace it with certainty, but there are indications in the sections that the lumen penetrates even further. It is extremely difficult to ascertain the exact shape of the lateral ends of the lobes, as they are wedged in between several other tissues, and it is just possible that they are bilobed and not rounded as I have drawn them. That portion which could be followed with certainty is drawn with plain lines, and the uncertain parts are indicated by the dotted outline in fig. 29.

In the third place, a short basal portion has been added, forming a hollow stalk or pedicel (*ped.*) connecting the whole apparatus with the outer epithelium. This pedicel is supported on each side by a chitinous rod-like thickening (*rd.*) in the form of a fold springing into the lumen from the lateral edges of the chitinous lining and corresponding to the "prolongement chitineux" described by Schimkewitsch ('84, p. 66, Pl. ii, fig. 6) in the adult of *Epeira*.

The small entochondrite (*t.*), which in fig. 28 is attached to the hypodermis near the extreme lateral ends of the spiracle, is now found a long way off from the spiracle. By comparing the two figures it will be seen that the entochondrite has not actually changed its position but that the spiracle (*sp.*) itself has greatly contracted, being now, in fact, less than half its former width, and thus the tissue bounding its lateral ends now comes to lie some distance away from the entochondrite. In shape this entochondrite (*t.*, fig. 29) has greatly elongated. It is broader towards the ends and slenderer just behind the middle and is attached at its posterior end (at *x*) directly to the hypodermis. To the larger anterior portion three muscles are attached, viz. the anterior oblique muscle (*a. ob. m.* 10) and two other muscles, the medial and lateral spinner muscles (*m. sp. m.* 10 and



*l. sp. m.* 10), which pass posteriorly and attach themselves to the medial and lateral parts respectively of the base of the left anterior spinner. The same muscles are seen in fig. 28. The smaller posterior portion of the tendon is further connected with the lateral edge of the tracheal pedicel by a small transverse column of cells (*tr. m.*), apparently of a muscular nature and plainly corresponding to the little tracheal muscle found by Schinkewitsch ('84, p. 66, Pl. ii, fig. 6)<sup>1</sup> and subsequently also by Lamy (:02, p. 160, Pl. viii, figs. 4, 5) in the adult of *Epeira*. Schinkewitsch considers these muscles to serve the purpose of closing the lumen of the tracheal pedicel, which in the adult, as well as in the young, is strongly compressed dorso-ventrally. The lateral part of the tracheal proliferation lies under the two spinner muscles and the entochondrite, *t.*, and the posterior edge of the proliferation is apparently wedged in between the spinner muscles and the transverse tracheal muscle.

The lumen of the whole trachea at this stage is lined with a smooth but strong cuticular membrane (*cu.*, fig. 29A). The great ventral longitudinal muscles (*v. l. m.* 10) of the tenth somite are stretched some distance above the trachea between the entochondrites *t.* 9 and *t.* 10. The former of these entochondrites is attached as before to the anterior end of the tendinal portion of the trachea (*ec. t.* 9), while the latter lies above the spiracle and is attached to a long hollow entapophysis from the posterior side of the anterior pair of spinners.

After the second post-embryonic moult (stage 9) the tracheæ appear for the first time as a fully functional respiratory organ. In shape they are not much changed, except that the lateral proliferations now branch at the ends into two smaller tracheæ, but beyond these I could not find any other branchlets at this stage. The chitinous lining is now covered (except in the pedicel) with the palisades of hooped (anastomosing) spines, also found in the adult spider, which keep

<sup>1</sup> In the figure the muscle is marked *ep.*, but in the text (p. 88) these letters stand for the chitinous thickening.

the lumen permanently open and allow the air to circulate freely through it.

The anterior (ventral) and posterior (dorsal) walls of the pedicel are close together and lined with a smooth, stout, chitinous membrane, but the two main tracheal trunks are now connected by a spined intertracheal canal of communication, exactly resembling the similar canal already described for the lungs.

I have no other stages between this and the adult form, the chitinous skeleton of which is drawn in fig. 31, and may be readily derived from the post-embryonic stages just described. In fact the only essential difference between the adult form and that after the second moult consists in the presence in the former of a large number of fine tracheal tubules or secondary branchlets, which spring from the main trunks either singly or in clusters, particularly from the ends of the tendinal trunks and of the two branches of the lateral trunks.

The entochondrite (*t. 9*) of the earlier stages is now found attached to the apex of a main tendinal trunk (*m. tr.*), which is not continued beyond the entochondrite in this species except in the form of a bunch of fine tubules.

In *Attns*, therefore, the two main tracheal trunks (*m. tr.*, fig. 31) are serially homologous with the pair of entapophyses or ectodermal tendons (*ec. t.* 8, fig. 20), to which the entochondrites of the ventral longitudinal muscles of the pulmonary and tracheal somites are attached, and are actually homologous with the corresponding entapophyses of the second pulmonary segment of *Tetrapneumonous* spiders.

The lateral basal lobes (*l. tr.*, fig. 31) of the tracheæ are directly derived from the lateral proliferation of the earlier stages, and are serially homologous with the pulmonary sacs of the previous segment, and are to be considered as actually homologous with the pulmonary sacs of the second pair of lung-books of *Tetrapneumonous* spiders.

**Critical remarks on the literature.**—Schimkewitsch was the first to figure a stage in the development of the trachea of a spider, for in his Russian paper ('86a) he gives a sketch (fig. 29A) of what is evidently the tendinal portion of the trachea (*ect.*) and the entochondrite (*L.* 2) attached to it. I am unable at present to consult his principal paper on the development of Spiders ('87), but apparently Schimkewitsch failed to recognise the tracheal nature of the ectodermal tendon, *ect.*, which he considered to be a provisional structure, as is evident from the following remark in a later paper ('94, p. 210): "Bei den Araneiden, wo das Endoskelet im Abdomen fehlt, entstehen beim Embryo unter den hintern Sehnen provisorische Ectodermfalten, die von mir auf fig. 11, tab. 22 ['87] abgebildet sind." By "Sehnen" the author refers to the entochondrites of the ventral longitudinal muscles.

Simmons ('94) gives two figures of the developing trachea. His earliest stage (fig. 8) is a sagittal section cut at a period when the tracheal appendages are on opposite sides of the embryo (my stage 5). It, therefore, represents a section through the dorsal proliferation of the tracheal sac, and is, as Simmons correctly claims, homologous with the pulmonary sac. On the other hand, his second figure (fig. 9), cut after the reversion, evidently represents the tendinal portion of the trachea, and cannot be the same structure as that represented in fig. 8, as Simmons claims it to be.

Simmons also claims to have found rudiments of the pulmonary folds, and interprets certain undulations on the surface of the embryonic trachea and two in-pushings at its ends (fig. 8) as such, but without, I think, sufficient justification for doing so. Similar undulations may be found in *Attus floricola* (e. g. on the posterior surface of appendage 2 in fig. 5), which certainly bear a superficial resemblance to the pulmonary folds in appendage 1, but these undulations are produced by the mitoses of nuclei lying quite near the surface, and may occur on any part of the body. They have certainly nothing to do with pulmonary folds. Also, the two in-pushings

figured by Simmons do not resemble pulmonary folds, being on the opposite sides of the tracheal tube, and they can hardly be "tracheal twigs" as Simmons suggests, since the lateral tracheæ are, I believe, unbranched in the two forms examined.

**The Attus-type and similar types of tracheæ in other spiders.—**

The Attus-type of tracheæ has been found in various other genera of Attidæ (Bertkau, Lamy), and is possibly the prevailing type in this family.

A very similar type, not sharply separable from the Attus-type, has been described by Bertkau and Lamy under the name arborescent type of tracheæ, on account of the more frequent branching of the twigs given off by the main trunks. Other differences, according to Lamy, are the presence of a spiral thread in the main trunks, and the prolongation of these trunks into the cephalothorax. Such tracheæ have been found in the Uloboridae (Uloborus, Lamy, :02, fig. 3, Miagrammopes, fig. 5), Prodidomidæ (fig. 26), Zodariidæ (Zodarion, fig. 31), Clubionidæ (Anyphæna, fig. 51) and Attidæ (Ballus, fig. 67).<sup>1</sup>

In all these forms the main trunks probably represent the entapophyses, while the small, branched, lateral lobe at the base of each trunk is, no doubt, the rudimentary homologon of a pulmonary sac, exactly as in Attus floricola.

Lamy failed to recognise the homologon of the pulmonary sacs in these lateral lobes in the arborescent and Attus-types of tracheæ, and supposed that here the ectodermal tendons and the lateral trunks (representing the pulmonary sacs) were completely fused together and no longer distinguishable. He also strangely misunderstood my statement on the subject, for he quotes (:02, pp. 257 and 260) me as having said that in the Attidæ the homologon of the pulmonary sac takes no part in the formation of the tracheæ, which are entirely formed of the entapophyses, and he then proceeds to dissent from this view.<sup>2</sup> My actual statement

<sup>1</sup> The figures referred to are all in Lamy (:02).

<sup>2</sup> Thus on p. 260 he says: "En tout cas, l'opinion de Purcell sur les

was ('95, pp. 398, 399): "The homologon of the lung is represented in the latter groups [Agelenidæ, etc.] by the lateral pair of tracheal trunks, but in the Attidæ by a mere rudiment in the form of a short lateral process on each side at the base of the two large trunks."<sup>1</sup> There was, therefore, no need to have differed from me as to the presence of the homologa of the lungs.

**The Agelena-type of tracheæ and its development.**—It was shown long ago, first by v. Siebold ('48) and later by Bertkau ('72, '78) and Lamy (:02), that many families of Dipneumonous spiders (about half of the genera examined, according to Lamy, p. 227) possess a much simpler tracheal system than that which occurs in the Attidæ. This simplified system<sup>2</sup> consists of four long trunks united behind at the base, as in fig. 21, but without any of the fine secondary tubules found in the Attidæ.

Such tracheæ occur in the Agelenidæ, Clubionidæ, Drassidæ, Argiopidæ, Lycosidæ, Theridiidæ, etc., and their relation to the Attus-type of trachea may be at once seen by comparing fig. 21 (*Tegenaria*) with fig. 29 (young *Attus*). Here the tendinal trunks (*m. tr.*) in the latter are obviously equivalent to the medial pair of trunks in *Tegenaria*, while the lateral branch (*l. tr.*) on each side in *Attus* is represented by the pair of lateral trunks, which, therefore, are serially homologous with the dorsal proliferation of the embryonal pulmonary sac.

That this is really the case may also be easily shown from the embryological material of *Agelena labyrinthica* in my possession. Shortly before the hatching of the embryo and after the completion of the reversion in this species, the pair of tracheal plates have very much the same form as in

trachées des Attidæ, auxquelles il donne une origine entièrement entapophysaire, ne me semble pas acceptable."

<sup>1</sup> On p. 248 Lamy curiously enough correctly quotes this statement.

<sup>2</sup> Literature: v. Siebold ('48, p. 535), Leydig ('55, p. 460), Bertkau ('72, '78), Schimkewitsch ('84), W. Wagner ('88, figs. 26, 67, and 68), Vogt ('89, p. 226), Lamy (:00, :01, :02).

*Attus floricola* (fig. 28) at the same stage (stage 6). They are, however, much further apart, and, therefore, with a wider intertracheal infolding connecting them, the lateral proliferations being also more pronounced. Further, each plate is much thinner in the middle and lateral region than at the base and along the anterior and medial margins.

In embryos one to two days after hatching (stage 7) the tendinal portion of each plate has considerably increased in length and is, like the rest of the plate, very thin, except at the apex, where it rather suddenly swells out and ends in a thick knob to which the entochondrite is attached.

After the first post-embryonic moult (stage 8) the tendinal portion of the trachea has much the same appearance as in the previous stage, except that it has increased in length, but the lateral proliferations have grown for some distance in a lateral direction close to the hypodermal covering of the body and are now provided with a distinct lumen in the form of a very fine canal lined with chitin and communicating with the spiracle. The chitinous lining both of this and of the tendinal portion is smooth at this stage.

At the second moult (stage 9) the trachea assumes its permanent shape. The chitinous lining, except in the pedicel, becomes provided with the usual anastomosing spines and the lateral proliferations increase considerably in length, still growing in a lateral direction. The pedicel and the canal of communication also appear. In fig. 30 (just before the second moult) the hooped spines (*spi.*) of stage 9 have already appeared in readiness for the moult.

Both in this stage and in the previous one the lumen of the lateral proliferation (*tr. prol.*, fig. 30), in its basal region at least (i. e. near the pedicel), is eccentric, lying posteriorly to the axis, the posterior wall of the trachea being much thinner than the anterior wall, which contains nearly all the nuclei. Towards the apex this wall becomes much thinner and the lumen lies practically in the middle. This eccentricity of the lumen is significant of the origin of the lateral trachea, and may be at once understood if we remember that



the thicker anterior wall of the trachea is equivalent to the anterior wall of the pulmonary sac together with the lung-saccules produced by the latter.

Three forms of this type of trachea are mentioned by Bertkau ('72), namely, those having: (1) the two median trunks united at base to a short common tube, as in the Theridiidæ and some Argiopidæ (Bertkau and Lamy); (2) a medial and lateral trunk united at base in pairs on each side to form two short common trunks, as in Tegenaria (fig. 21), this being the usual form, according to Bertkau and Lamy; and (3) the four trunks springing separately from the pedicel, as in some Argiopidæ, e. g. Linyphia (fig. 25).

The resemblance between this third form of tracheal system (fig. 25), in which the lateral trunks at first take a lateral course before running forwards, and the pulmonary system of an Attus (fig. 20) is very striking, and clearly shows the homology of the medial trunks (*m. tr.*) with the entapophyses (*ec. t.* 8), and of the lateral trunks (*l. tr.*) with the pulmonary sacs (*pulm. s.*). The parallel between the spinous intertracheal canal of communication (connecting the median trunks with one another and with the lateral trunks at their base) and the interpulmonary canal of communication (connecting the entapophyses with one another and with the pulmonary sacs) is complete, as may be seen by comparing fig. 24 with fig. 23 (sagittal sections through the lateral region of the canal [*can.*] along the lines indicated in figs. 25 and 20), and fig. 26 with fig. 23B (median sections along the lines indicated in figs. 25 and 20). From these figures it will also appear perfectly clear that the medial trunks of the tracheal system cannot be considered as branches of the lateral trunks any more than the entapophyses of the pulmonary segment are branches of the pulmonary sac.

In the Agelena-type of tracheæ the medial trunks generally take a fairly straight course as far as the ento-

chondrite, where they may either terminate and thus remain comparatively short, as in *Araneus* (*Epeira*), according to Lamy, or they may become longer and be continued beyond the point of attachment on the lateral side of the entochondrite, often winding about for a short or even a considerable distance further before coming to an end (*Agelena*, *Tegenaria*, *Melanophora*, *Pachygnatha*, *Clubiona*, etc.). These long trunks are frequently bifid for some distance from the apex, a character first observed by W. Wagner ('88) in *Lycosa*, and subsequently by Lamy (:02) in several other forms (*Agelena*, *Zora*, *Tibellus*, etc.).

The form with short medial trunks has been carefully studied by Lamy (:02), who was the first to describe the method by which these trunks are attached to the entochondrite. The tendinal trunks, according to Lamy, are produced at their ends into a chitinous fibrous piece which adheres to the entochondrite and is not furnished with a spinous cavity and therefore presents "absolument un aspect entapophysaire ou tendineux" (:01b, p. 178). This fibrous termination was observed by Lamy in most *Theridiidæ* and various *Argiopidæ* (*Linyphia*, *Araneus*, etc.).

The form of trachea with long medial trunks is very widely distributed, but its mode of attachment to the entochondrite has evidently eluded the observation of Lamy, for he nowhere makes any definite statement nor gives any figure regarding this point, except in the case of *Tegenaria*. In this genus the medial trunks are said to terminate at the entochondrite in the same fibrous process which was observed in the *Theridiidæ*, etc. (Lamy, :01b, p. 178), and one of the trunks is figured as ending in such a process (:02, p. 213, fig. 58).

I have examined five adult specimens of *Tegenaria domestica* after treatment with caustic potash, and always found the medial trunks evenly rounded off at the apex and spined internally to the very tip, but without any trace of terminal fibres. At a distance from the apex equal to about two fifths of the whole length I found one or more short,

fibrous, chitinous processes (*hy'*, fig. 42) attached to the medial side of the trunk, which undoubtedly represent the terminal fibres found by Lamy in *Araneus*, etc., and which connect the trachea with the entochondrite. The part of the trachea which is produced beyond the point of attachment is thinner than the part posterior to the entochondrite, and may be either a single tube as in *B*, fig. 42, or it may consist of two equal (left side, fig. 21) or unequal tubes (*br.*, fig. 42) produced by the branching of the main trunk at the insertion of the fibres. In one case each of the branches was again divided so that the tracheal trunk then ended in four separate points. There is no symmetry about this branching, for one side may be branched and the other not, but in all cases the branches are lined internally with hooped spines right up to their tips, differing in this respect from the ordinary secondary tubules of the *Attidæ*, etc., from which such spines are absent.

The only instance which Lamy mentions of a similar tendinous fibre being attached to one side of a medial trunk is the genus *Chorizomma* (:02, p. 219), in which, however, the tracheæ belong to a different type from the one we are now discussing.

It is probable that the various forms of tracheæ with long medial trunks, whether branched or not, described by Lamy in a number of families (*Drassidæ*, *Argiopidæ*, *Thomisidæ*, *Clubionidæ*, *Agelenidæ*, *Lycosidæ*, etc.), all resemble one or other of the variations of *Tegenaria* in their mode of attachment to the entochondrite.

In *Nephila*, which Lamy reckons with the forms with short medial trunks, I observed the tendinous fibres both at the apex and also on the medial side at some distance from the apex. This form may have, therefore, two places of attachment.

In all cases these medial fibres, and a good part of the terminal ones, are certainly nothing else but the intercellular fibres usually produced by the hypodermal cells of an entapophysis to connect the cuticula with the attached entochondrite or muscle (e.g. *hy'*, figs. 32, 36, etc.). They do not

themselves constitute the entapophysis, which is, of course, formed by the entire ectodermal invagination—that is to say, in this case the medial tracheal trunks.

**The tracheæ in the Dysderidæ.**—These tracheæ, which have been frequently described,<sup>1</sup> were the first found in spiders (by Leon Dufour<sup>2</sup> in 1834, teste Bertkau, '72, and Lamy, :02), and are of considerable interest from a comparative anatomical point of view. I have myself examined sections of *Segestria*, *Harpactes*, and *Dysdera*.

The tracheal spiracles of the *Dysderidæ* are widely separated, lying in the anterior region of the body a little behind the pair of pulmonary spiracles (text-fig. 3, p. 69), and entirely unconnected with one another. Each leads into a large tracheal trunk, which rises upwards from the spiracle and then runs forwards and breaks up at its anterior end, either in the pedicel of the abdomen or a little behind it, into a large bunch of fine secondary tubules. At the base a shorter posterior trunk projects backwards, and also gives off a number of fine tubules. The chitinous lining of the trunks is provided with spines, which support a spiral thread (*Dysdera*) or an inner perforated tube (*Segestria*).<sup>3</sup> To these well-known facts I have to add the following observations :

The segments of the ventral longitudinal muscles belonging to the tracheal somite are very short in this family, like the somite itself, and the entosternite is attached on the medial

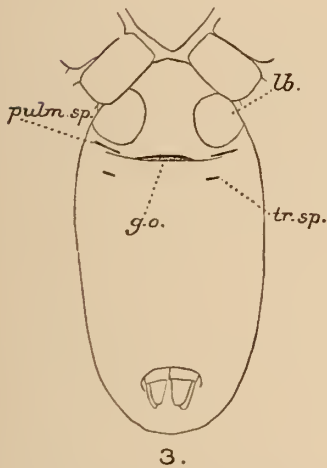
<sup>1</sup> Literature: Dugès ['36, '49; v. Siebold ('48, p. 535) also cites the following of the year 1835: 'Feuill. Acad. des Sci. Séance du 9. Févr.,' also Froriep's 'Notizen,' xliii, p. 231, also 'Ann. Sc. Nat.,' vi, p. 183]. Bertkau ('72), MacLeod ('80), Lamy (:02).

<sup>2</sup> I am unable to find the reference to this paper, unless it be 'le Temps,' No. 1942, cited by Menge ('51, p. 22), which, however, v. Siebold ('48, p. 535) accredits to A. Dugès, both authors giving the year 1835, and not 1834.

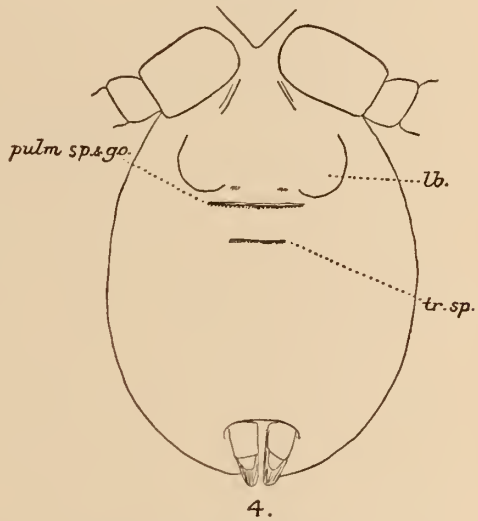
<sup>3</sup> Bertkau ('72) states that in *Segestria* these spines do not anastomose, but Lamy (:02, p. 183, fig. 23) has since shown (and I can corroborate his statements) that they certainly anastomose at their ends, forming an inner, fenestrated, chitinous tube. In *Harpactes* the anastomosing branches of the spines form a simple network only.

side of the base of each tracheal pedicel. In *Segestria* the ectodermal area of attachment is drawn out in a mediad direction in the form of a short, flat, unspined pouch (*ec. t.* 9, figs. 32 and 33), which opens into the short, smooth, flexible pedicel (*ped.*) connecting the rigid outer cuticula (*cu.*) with the spinous main trunk (*tr.*) of the trachea. This entapophysis is not respiratory, and the entire trachea is to be regarded as homologous only with the embryonic pulmonary

TEXT-FIG. 3.



TEXT-FIG. 4.



*Segestria senoculata*, ♀.      *Argyroneta aquatica*, ♀.

Ventral surface of abdomen.—*pulm. sp.*, pulmonary spiracle; *tr. sp.*, tracheal spiracle; *lb.*, operculum of lung-books; *g. o.*, genital opening; Magn. 12.

sac and its proliferation, as I have already stated in a previous communication ('95). That this must be the case may fairly be concluded from the position of the pair of spiracles (text-fig. 3) corresponding to the second pair in *Tetrापneumonous* spiders (text-fig. 2, p. 52) and from the position of the entapophysis on its medial side. Lamy (:02) has also expressed himself in agreement with this view, which differs entirely from that of Bertkau ('72), who considered the short posterior

trunks only to be equivalent to the lateral trunks in other spiders.

**The tracheæ in *Argyroneta aquatica*.**—The highly-developed tracheæ<sup>1</sup> of this water spider are very peculiar. The two main branches, as Bertkau ('78) showed, have a common spiracle, which opens far forwards (text-fig. 4), close to the pulmonary spiracles. The remarkable point about these tracheæ is the circumstance that they lie entirely on the medial side of the longitudinal ventral muscles. The segment of this muscle belonging to the tracheal somite is very short, corresponding to the anterior position of the spiracle, and it is stretched between two large entochondrites, the posterior of which is attached to the upper surface of a short basal process on the lateral side of the tracheal trunks. This process, which is figured by Lamy (:02, p. 212, fig. 56), is provided in its cavity with spines, like the main trunks, and gives off at its apex a number of fine tracheal tubules (the lateral bunch of tracheæ described and figured by Menge ['51, *dd*, Pl. i, fig. 7] and Lamy).

The process is flattened dorso-ventrally and corresponds to the tendinal trunk of other Dipneumonous spiders. The two large main trunks appear to be outgrowths from the medial side of each very short tendinal trunk. They are joined at their bases by an intertracheal fold provided with the usual spinous canal of communication. On the posterior side of each main trunk, near its base, is a transverse out-folding of the tracheal wall forming a deep spinous groove on the inside of the trachea, connecting the canal of communication with the lateral or tendinal branch. This transverse folding, which was described by Lamy (:02) as an abdominal trunk resembling that in *Segestria*, also gives off numerous tubules, which, together with another group just below, springing directly from the main trunk, form the posterior bunch of tracheæ figured by Menge ('51, *ee*., Pl. i, fig. 7).

In *Argyroneta*, therefore, the entire tracheal

<sup>1</sup> Literature : Grube ('42), Menge ('51), Bertkau ('78, p. 384), MacLeod ('80, '84), Lamy (:02).



system appears to be derived from the tendinal portion of the trachea, and there is no distinguishable trace left of the lateral trunks, which may be homologised with the pulmonary sac.<sup>1</sup> This leads us to the conclusion that the tracheal systems of *Argyroneta* and the *Dysderidæ*, although superficially closely resembling one another, are yet apparently not homologous structures.

**The tracheæ in the *Scytodidæ*, *Palpimanidæ* and *Filistatidæ*.—**The tracheæ of these three small families possess a peculiar interest, inasmuch as Lamy has shown that their medial trunks are non-respiratory and serve solely as entapophyses for the attachment of the entochondrites. Bertkau ('78) observed that the medial trunks were reduced to an unpaired median rudiment in *Scytodes*, only the lateral ones being developed, but our knowledge of the tracheæ in the other forms is due to Lamy (:00, :01b, :02).

The most interesting is the tracheal system of *Filistata*, of which I reproduce Lamy's figure (:02, p. 173, fig. 12), as I have no material of this family at my disposal. Here, according to Lamy's description, the spiracle is very broad and placed about midway between the interpulmonary fold and the spinners. The two short lateral trunks (*l. tr.*) are pointed sac-like and of the simplest form, exactly as a pulmonary sac would appear if it lost its saccules. The four trunks are connected at base by an intertracheal fold with spines in its deepest part (which no doubt forms a canal of communication). The two entapophyses (*ec. t.* 9), too, have some internal spines in their basal part, but are otherwise unspined, while their free ends are jagged and tendon-like. If we compare this text-figure with the figure of the pulmonary system of *Attus* (fig. 20) and leave the saccules out of account, the parallel between the two

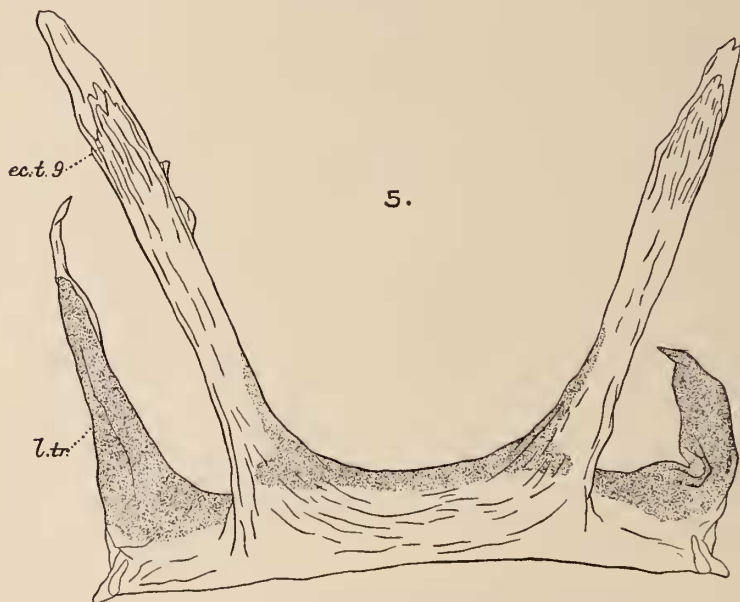
<sup>1</sup> MacLeod's ('82, p. 785, and '84, p. 29) view that the trachea of *Argyroneta* is nothing else than the dorsal chamber of the second pair of lung-books of a *Mygale*, enormously developed, is certainly incorrect.

respiratory systems appears complete and their homologies almost self-evident.

In the Palpimanidæ, according to Lamy, the medial trunks are separate at least at their apex, while in the Scytodidæ they are confluent to the apex and form a single median trunk.

I have examined preparations in caustic potash and sections

TEXT-FIG. 5.



*Filistata capitata* Hentz. Tracheal apparatus (after Lamy). *ec. t. 9.*, entapophysis; *l. tr.*, lateral tracheal trunk. Magnified 100.

from both families. The long, lateral trunks are connected by a canal of communication (*can.*, fig. 38), lined internally with hooped spines (*spi.*), which also spread into the basal part of the median trunk. This latter is unpaired, and although in my examples of *Palpimanus* there are indications of a bifurcation at the apex, it is not nearly so prominent as in the species figured by Lamy (:02, p. 187, fig. 29).

The median trunk is flattened dorso-ventrally and hollow

internally nearly to the apex, but its chitinous lining is plainly much too thick to allow it to be used for respiratory purposes. In *Scytodes* by far the greater portion of this chitinous lining is smooth internally (figs. 38 and 39), only a small part quite at the base being spined (*spi.*, fig. 38), but in *Palpimanus* nearly one half is lined with hooped spines (fig. 37A). In both genera the greater part of the unspined portion of the entapophysis is in contact with the entochondrites (*t. 9*, fig. 37).

The histological structure of these tracheal entapophyses and of those of the pulmonary segment of *Attus* is quite similar. The section through the basal half of the tracheal entapophysis of *Palpimanus* (fig. 37A) should be compared with the spinous part (*spi.*) of the pulmonary entapophysis given in fig. 23A (in the latter the matrix is not drawn in), while fig. 37 of *Palpimanus* is comparable with fig. 23 of *Attus*, both passing through the places of attachment to the entochondrites, *t. 9* and *t. 8*. The same fibrous hypodermis (*hy.*) and flattened smooth cuticula (*cu.*) is observable in both figures.

In his description of *Palpimanus gibbulus* Lamy says there are two short medial apophyses without a spinous lining (:02, p. 188), but his figure clearly shows that the two trunks are confluent for the greater part of their length and separate only towards the apex. Lamy evidently considers the confluent portion to be part of the vestibule. In other places, too (:01b, p. 178; :02, p. 174), he states that in all these forms the medial trunks are reduced to the unspined, terminal, tendinous (i. e. fibrous) part found at the end of the medial trunks in *Epeira*, etc., by means of which the attachment to the entochondrite is effected, while the whole portion of the trachea in *Epeira* between the entochondrite and the vestibule are said to be absent in *Palpimanus*. I cannot consider this view to be quite correct, for the entire median process in *Palpimanus* and *Scytodes*, including the unpaired part in the former and the spinous portion in both, constitutes the entapophyses, and the spinous portion lying

between the entochondrite and the vestibule is homologous with the much longer but corresponding portion of the medial tracheal trunks in *Araneus*, *Tegenaria*, etc.

Thus, the medial trunks in *Filistata*, *Palpimanus* and *Scytodes* are homologous with the entire medial trunks in *Araneus*, etc., and not merely with their unspined, fibrous, apical portion, as Lamy suggests.

The unspined portion of the medial trunks in *Filistata*, *Palpimanus* and *Scytodes* may well be compared to the tracheae of a young spider previous to the second moult (stage 8), while this organ is still in its primitive spineless condition. (Compare the transverse section, fig. 29A, of the medial tracheal trunk of a young *Attus* with that of the cuticular lining of the entapophysis of *Scytodes* given in fig. 39.)

In the pulmonary segment the unpaired median entapophysis of a *Scytodes* has its exact parallel in the unpaired median entapophysis of such forms as *Lycosa Darlingi*, described on p. 51. We thus see all the variations of the pulmonary entapophyses repeated in the tracheal segment.

#### IX. THE ENTAPOPHYSES OF THE THIRD AND FOURTH ABDOMINAL APPENDAGES (THE SPINNERS).

These tendons are unconnected with the respiratory organs and need only be briefly described. They arise at a very early stage, being formed out of the post-appendicular grooves (*gr.*, fig. 4), which appear behind the third and fourth pair of abdominal appendages shortly before the beginning of the reversion (stage 1). At the time of the appearance of the first pulmonary furrows (stage 2) these grooves have deepened and become more pronounced (figs. 5 and 5A), and they may be easily followed through all the later stages (fig. 6).<sup>1</sup> At the end of the reversion they form invaginations (*ec.*

<sup>1</sup> I may point out that no trace of a lateral proliferation corresponding to that of the pulmonary and tracheal sacs is ever found in connection with these grooves.

*t.* 10 and 11, fig. 41), which may exceed that of the proctodæum (*proc.*) in size. After moulting they form internal cones or processes with a chitinous axis situated at the posterior inner angle of the anterior and posterior spinners respectively. At the stage of fig. 29 (stage 8, after the first moult) the entochondrite (*t.* 10), to which the anterior of these entapophyses is attached, is placed just over the tracheal spiracle, but is, of course, not attached to it.

The chitinous skeletons of the entapophyses of an adult *Tegenaria* and their relation to the anterior and posterior spinners are shown in fig. 21. These spinners are, of course, the third and fourth abdominal appendages, but the middle pair of spinners (*m. spin.*) do not, according to Jaworowski ('95), correspond to a pair of appendages and have consequently no entapophyses. An entochondrite of the longitudinal muscles is attached to the anterior part of each of these entapophyses, the posterior of the three well-known pairs of large abdominal entochondrites<sup>1</sup> described by Schimkewitsch ('84, p. 38) and others being that (*t.* 10) which is attached to the entapophyses of the anterior pair of spinners.

The four pairs of serially homologous entapophyses (*ec. t.* 8-11) may all be seen in fig. 21. They are, of course, connected on each side by a longitudinal muscle, and the positions of the four intermuscular tendons (*t.* 8-11) are indicated in brackets. This figure may, therefore, serve to give a general idea of the inter-relationship of all these tendons of ectodermal (*ec. t.* 8-11) and mesodermal (*t.* 8-11) origin.

## X. GENERAL CONCLUSIONS.

The embryological data furnished in the preceding pages will, I believe, enable us to arrive at definite conclusions with regard to certain questions concerning the phylogenetic

<sup>1</sup> These three entochondrites, marked *l2*, *l1*, and *l3* in Schimkewitsch's Pl. vii, fig. 1, correspond to *t.* 8, *t.* 9, and *t.* 10 respectively in my fig. 41.

origin of the tracheæ, as well as of the lung-books in *Araneæ*.

**The origin of the tendinal or medial tracheal trunks in *Araneæ*.**  
—As the pair of ventral longitudinal muscles is a very primitive structure, and must originally have been attached to the outer hypodermis, it follows that the tracheal nature of the tendinal or medial tracheal trunks must be a secondary character, for if this were not the case we should have to assume that all the ectodermal areas of attachment of the ventral longitudinal muscles were originally derived from tracheæ, since they are all serially homologous, but this would be an absurd supposition and quite contrary to the facts of embryology and comparative anatomy.

I have also already pointed out that these medial trunks cannot be considered as branches of the lateral ones, nor does the embryological evidence show that they are otherwise than independent metamorphosed entapophyses united at their base with the lateral trunks by an intertracheal fold and canal of communication, exactly in the same way as the entapophyses of the pulmonary segment are united with the pulmonary sacs by an interpulmonary fold and canal of communication. The independent nature of the tendinal trunks is obscured in the adults of such forms as the *Attidæ* (fig. 31), owing to the partial fusion of the rudiments of the lateral trunks with the base of the medial ones, but it is clear enough in most other forms. Even in such forms as *Segestria*, *Scytodes*, and *Palpimanus*, where the entapophyses have not been converted into tracheæ, they remain attached to the smooth pedicel at the base of the lateral tracheæ (*Segestria*, fig. 32) or to the spinous canal of communication uniting the two lateral trunks (*Scytodes* [fig. 38], *Palpimanus*), and do not shift their position on to the spinous part of these trunks. These forms, therefore, do not provide us with any grounds for supposing that the spinous parts of the medial trunks in other spiders have originated as outgrowths from the spinous part of a lateral trunk. In fact, we have no other alternative, in view of



both the embryology and comparative anatomy, but to consider the medial trunks of the tracheæ as equivalent in their entirety to metamorphosed entapophyses.

It is, moreover, a common feature in the Arachnida for the ectodermal areas of attachment of various muscles to be invaginated into the body in the form of pouches or tubes for the purpose of serving as tendons, as, for instance, the entapophyses (*ec. t.* 10 and 11, fig. 21) of the two following abdominal segments already described.

In order that an ectodermal tendon may become converted into a trachea it is only necessary that it should be hollow and sufficiently thin-walled, with free access of air to its interior, and that it should lie in blood or tissues requiring aëration. It is also evident that a tendinal trachea must have existed first as a simple entapophysis, since it could not possibly function as a trachea until after it had attained a tubular form. The entapophyses could not, therefore, have been originally produced for respiratory purposes.

In the case of Araneæ I have already sought to explain the elongated tracheal entapophyses by the great elongation of the ninth somite, and since the tubular entapophyses so produced are hollow and lie in the large ventral blood sinus (*v. sin.*, figs. 41 and 43) we have here all the conditions necessary for their conversion into a trachea. For it is well known that the blood passes from this sinus to the lung-books and thence to the heart, and that the sinus, therefore, contains venous blood requiring aëration (Blanchard '49, '50, Claparède '63, Schneider '92, etc.).

In the Tetrapneumonous spiders and in some Dysderidæ (Segestria) we find the rudiments of the entapophyses of the ninth segment in the form of shallow depressions (*ec. t.* 9, text-fig. 2, p. 52) or pouch-like invaginations (*ec. t.* 9, fig. 32), already described on previous pages. These rudiments have no respiratory function, and if they were to approach near to the median line and be united at base by an intertracheal infolding we should obtain the conditions found in Filistata,

etc. (text-fig. 5, p. 72), and we have only to further imagine these entapophyses lengthened and to become thin-walled and provided internally with spines throughout in order to convert them into the tendinal tracheæ of other Dipneumonous spiders. It is evident that the condition in the Tetrapneumonous spiders, at any rate, is a primitive one, on account of the other primitive characters of this group, but the possibility of a reversion from an elongated tracheal tendon back to a very short one must be borne in mind, and may, perhaps, occur in some Dipneumonous spiders in which the ninth somite has secondarily become shortened again. I do not think that this has been the case in the Dysderidæ, however, on account of the primitive position of the tracheal spiracles (text-fig. 3, p. 69) and other primitive characters in this family, but in *Argyroneta* (text-fig. 4, p. 69) I believe there is every probability that the spiracle was once more posterior and has subsequently shifted forward again to suit a newly acquired, aquatic habit. This would account for the fact that, although the actual tracheal entapophyses are extremely short, they are lined with the usual anastomosing spines and provided with a large medial outgrowth. This outgrowth may originally have been merely a medial prolongation of the tracheal entapophysis beyond the entochondrite, and when the spiracle moved forwards and the entapophysis shortened, its medial prolongation may have increased in inverse proportion, so as to maintain the effectiveness of the entire trachea as a respiratory organ.

It would certainly appear that the tendinal trunks are more effective breathing organs than the lateral trunks are, probably on account of the position of the former in the great ventral sinus of venous blood. For we frequently find the tendinal trunks very strongly developed, and the lateral ones correspondingly reduced to a mere rudiment (*Attidæ*) and sometimes apparently to vanish altogether (*Argyroneta*).

**The origin of the lateral tracheal trunks in *Aranæ*.**—The second question to be considered is whether the pair of lateral tracheæ of Dipneumonous spiders was derived from the second

pair of lung-books of Tetrapneumonous forms or whether the reverse was the case.

That the lateral tracheæ are serially homologous with the pulmonary sacs of the preceding somite and, therefore, homologous with the same part of the lung-books of the ninth somite in Tetrapneumonous spiders, cannot, I think, be disputed, although the embryology of the latter group is not yet known.

In deriving the lung-books from tracheæ the simplest theory and the one that has been usually adopted by those who favoured this view, is to consider the pulmonary sac or antechamber to represent the main trunk of a trachea and the saccules merely modified lateral branches arranged in a single row and flattened by mutual pressure.

A very serious objection to this view lies in the appearance of the two oldest pulmonary saccules on the embryonic appendages quite outside of the pulmonary sac. These two saccules cannot be branches of the main trunk, and in order to account for their presence we should have to assume that they themselves at one time each represented a separate tracheal trunk. This, however, could hardly have been the case, since all the saccules are formed in the embryo in exactly the same manner (apart from their position out of or within the sac) and should, therefore, have exactly the same phylogenetic origin.

Another view based by Jaworowski ('94) on embryological grounds and adopted by Bernard ('96, p. 375) on theoretical ones is to the effect that the lung-books arose by horizontal folds in the basal part of a vertical tracheal trunk. Here also the appearance of the two oldest saccules, entirely outside of the pulmonary sac, is too strong an argument against our acceptance of this theory, which, moreover, Jaworowski has failed to prove embryologically, as I have already pointed out on a previous page (p. 33).

In fact the only way we can derive the saccules of lung-books from tracheal tubes which appears to me at all feasible is to assume that an ancestral form of the Araneæ possessed

abdominal appendages, on the posterior side of which were a number of separate tracheæ arranged in a row, and that these appendages were sunk into the body in later forms. The tracheated appendages of such an ancestral form would, in fact, be very similar to one of the transitional stages which Kingsley assumes for his theory of the origin of lung-books from gills (p. 27), but it would be totally different from anything actually found in the tracheal system of existing spiders.

From purely embryological considerations, therefore, and quite apart from the branchial theory of the origin of the lung-books, we have to assume that the pair of lateral branches of the tracheæ of the ninth somite in Dipneumonous spiders must have been derived from the pulmonary sac and not the reverse. This conclusion is, moreover, strongly confirmed by the fact that the Tetrapneumonous spiders, and particularly the remarkable genus *Liphistius*, are more primitive in their other characters than are the Tracheate spiders.

**The origin of the secondary tracheal tubules.**—The third question is the nature of the tracheal branchlets, those fine tubules (*tr. tub.*, fig. 31) given off by the main trunks in certain forms (*Attidæ*, *Dysderidæ*, *Argyroneta*, etc.). It is usual to consider these as homologous with the saccules of the lung-books, whatever view<sup>1</sup> may be taken of the origin of the latter. I think, however, that this homology is, for the most part, erroneous.

Since the pulmonary saccules occur only on the anterior side of the pulmonary sac, we should expect to find the tracheal tubules on the corresponding surface of the lateral tracheal trunks, but this is by no means the case.<sup>2</sup> Thus, in

<sup>1</sup> Except, however, Jaworowski and Bernard.

<sup>2</sup> In the remarkable anterior pair of tracheæ of the Apneumonous Family *Caponiidæ*, described and figured in Simon ('Hist. Nat. Araign.', 2<sup>e</sup> éd., i. pt. ii. pp. 326, 327, figs. 294 and 295, 1893) after Bertkau, the tubules are nearly all placed, however, on the anterior side of an oval ante-chamber, and here, no doubt, do correspond to pulmo-

the Dysderidæ, in which the entire tracheal system is probably derived from lung-books, we find the tubules arising in a dense cluster from the apex of the elongate trunks and from a small basal branch on the posterior side, but none from the anterior or under surface of the trunks. Further, in all tracheæ of the Agelena-type, which is that of the majority of the Dipneumonous families, the lateral trunks have no secondary branchlets at all.

On the other hand we find these tubules at various places on the tendinal trunks in the Attidæ and other groups (fig. 31), which shows that the tubules may arise anywhere on a tracheal trunk, when required, and quite independently of the pulmonary saccules, since in this case they could not have been derived from the latter. In *Attus floricola* there is no embryological evidence that the tubules of the lateral tracheal branches have anything to do with pulmonary saccules, for whereas these latter commence to form in the pulmonary segment at an early embryonic stage the tubules do not appear until long after the young spider has been hatched. It is, however, conceivable that the earlier lung-saccules may have been entirely suppressed in the tracheal segment, so that only the post-embryonic lung-saccules reappear as secondary tracheal tubules in certain cases, and the possibility of the anterior terminal tubules of the Dysderidæ and those of the lateral lobes of the Attidæ being of this nature must be borne in mind.

Bertkau ('72, '78) attempted to utilise the presence or absence of secondary tubules as the basis of a system of classification, but Lamy (:02) has shown that this character has little value for this purpose, since within the same family some forms may be provided with tracheal tubules, while closely related forms are entirely without them.

**The origin of the lung-books in Arachnids.**—A fourth question in connection with this subject is whether the lung-books of nary saccules, since the ante-chamber is doubtless that of the pair of lung-books which the tracheæ have replaced. I examined sections of *C. spiralifera*.

the Arachnids were derived in the first instance from tracheal books or from gill-books.

I have endeavoured to demonstrate in a preceding paragraph that, since all the lung-sacculæ within the pulmonary sac precisely resemble in their formation and structure the two oldest which appear outside of this sac, all the sacculæ must have had the same phylogenetic origin and must consequently all have originally been upon the posterior surface of the abdominal appendage. The question, therefore, is whether the sacculæ of this primitive appendage in the ancestral Arachnid were tracheæ or whether they were produced from sunken-in gill-lamellæ. Whereas the appearance of a number of tracheæ in such a position seems most improbable, the arguments in favour of the branchial origin appear overwhelming. Most important amongst these, next to the embryological evidence, is the undoubted general agreement and affinity between *Limulus* and Arachnida, first pointed out by Straus-Durckheim and v. Beneden, and afterwards so ably demonstrated by Ray Lankester. The embryological side of the question and the probable manner in which the transition from gill-books to lung-books may have taken place has already been fully discussed (pp. 17-44) and need not be considered again.

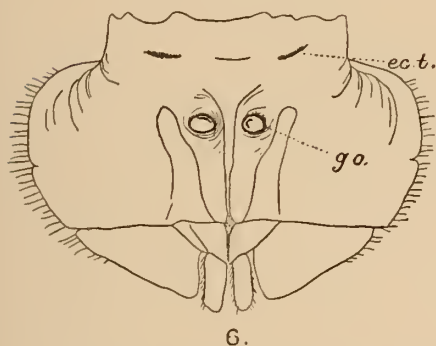
I shall only introduce here two figures of the abdominal appendages of *Limulus* for comparison with the pulmonary segment of a spider drawn in fig. 20. The appendages of the genital segment (text-fig. 6), which are homologous with those of the pulmonary segment, have no gill-books, but possess the pair of genital openings (*g. o.*), which would lie between the gill-books, if the latter were present. Text-fig 7 represents a branchiate appendage, and it will be seen that if the gill-leaves were sunk into the appendage and the latter into the abdomen, we should have exactly the condition found in a spider (fig. 20). The large entapophyses (*ec. t.*) shown in the text-figures are not, however, homologous with those of the pulmonary segment (*ec. t.* 8, fig. 20).

The endeavour to derive all tracheæ in Arthropods from a

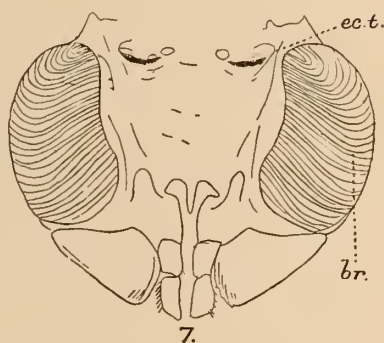


common origin has no doubt weighed considerably against the acceptance of the branchial origin of lung-books, but this should not be the case in view of the undoubted diphyletic origin of the tracheæ in Araneæ, which, I think, I have sufficiently demonstrated. Further, in one and the same spider both parts of the tracheæ, although of different origins, have exactly the same histological structure, hence similarity of structure in the fully developed tracheæ does not mean similarity of origin. I mention this here expressly, since this similarity of structure has been used as

TEXT-FIG. 6.



TEXT-FIG. 7.



TEXT-FIGS 6 and 7.—Appendages of the genital segment and a pair of abdominal branchiate appendages of *Limulus*, seen from behind (after Ray Lankester). *g. o.*, genital openings; *br.*, gill-book; *ec. t.*, external opening of an ectodermal tendon.

an argument in favour of the monophyletic origin of all tracheæ.

The appearance in spiders of tracheæ as newly acquired organs derived from two separate and distinct sources simultaneously with the occurrence of other well-developed organs of respiration clearly shows how readily tracheæ may be acquired.<sup>1</sup> Why, then, should they not have originated

<sup>1</sup> Pocock ('93), who was of opinion that tracheal tubes replaced lung-books at least twice in the group Arachnida, viz. in the Dipneumones and in the Pseudoscorpiones, remarks (p. 17): "The fact that these tubes have been developed twice in the same group bears very strong evidence as to their efficacy as breathing organs. They

equally readily over and over again in the Arachnida, and particularly in so large and diversified an assemblage as the Tracheata? Thus in the Solifugæ the thoracic tracheæ, which open at the base of the third pair of legs and have always been an unexplained anomaly in view of the branchial theory,<sup>1</sup> may easily have originated from the entapophyses of some muscle. The same remark applies to the occurrence of the remarkable pair of tracheal spiracles discovered by Hansen ('93, p. 198), and subsequently confirmed by Loman ('96) on the tibiæ of the four pairs of legs in the Phalangiidæ.<sup>2</sup>

I do not mean to imply that these abnormal tracheæ were

must, in fact, be better adapted for their purpose than the lung-book tracheæ." This remark of Pocock's may possibly explain why such highly segmented forms as the Solifugæ have highly developed tracheæ only, since the extraordinary activity of the members of this group would require the presence of the most effective breathing organs. Bernard ('96, p. 374) mentions that these are the only Arachnids in which the primitive tracheal tubes anastomose (as in the Insecta), and to this I may add an observation which I have often made on living Solpugidæ, which is that regular and pronounced respiratory movements are observable in the middle part of the body, especially after the animal has been running. Similar movements have not hitherto, so far as I am aware, been recorded for any air-breathing Arachnids (see Plateau, '86).

<sup>1</sup> Bernard ('92, p. 521), for instance, remarks that the presence of tracheæ on the cephalothorax in Arachnida is "one of the principle difficulties in the way of those who would deduce the Arachnidan abdominal tracheæ from embedded gills. . . . It compels us, for instance, to assume that the cephalothoracic tracheæ have had an entirely different origin, so that . . . it is necessary to assume that the same structures, tubular tracheæ, have had two independent origins in the same animal! . . . there is absolutely no difference between the tracheæ which open through the large stigmata of the thorax and those opening through the more insignificant stigmata in the abdomen [in the Solifugæ]. It is difficult to believe that they had a separate origin. The embedded gill theory must, I think, definitely give way before some simpler theory, such as that here put forward." So also Weissenborn ('87, p. 114).

<sup>2</sup> It is interesting to note that Loman found these spiracles absent in very young Phalangiidæ.

probably muscular tendons. They may have had any other origin. Thus J. Wagner ('94, p. 126), who has investigated the embryology of Acari and admits the branchial origin of lung-books, explains the cephalothoracic tracheæ of Acari and Solpuga by deriving them from unicellular hypodermal glands, such as are found in water mites; while Börner (:02, pp. 455, 461, and 463) considers it very probable that the spiracle on the prosoma is that of the genital segment displaced forwards. Further, Ray Lankester's suggestion that tracheæ may have arisen by the tubefaction of mesodermal strands may apply.

The primitive nature of the lung-books in comparison with the tracheæ within the class Arachnida is in full agreement with the teachings of the comparative anatomy of other organs. Thus we find only lung-books in the highly segmented orders Scorpiones and Pedipalpi, tracheæ in the orders with more concentrated bodies, Opiliones and Acari, while in the Araneæ the more primitive Tetrapneumones have lung-books only, the more highly specialised Dipneumones tracheæ as well. The Solifugæ, however, which are highly segmented, have tracheæ only (see footnote on p. 84).

Bernard's theory that tracheæ have arisen from bristle-sacs of Chætopod Annelids cannot be maintained for a moment as an explanation of the lung-books or tracheæ of Araneæ in spite of the resemblance which the ectodermal tendons of the tracheal segment in my fig. 41 bears to the bristle-sac with its two oblique muscles figured by Bernard ('92, text-fig. 1, p. 512). Indeed, Bernard does not attempt to derive entapophyses from bristle-sacs, and the rudimentary spiracles (vestigial stigmata) which he claims to have found in Pseudoscorpiones ('93a, p. 422, and '93b, p. 26) and Pedipalpi ('94, p. 151) are always placed by him on the lateral side of the depressions caused by the dorso-ventral muscles of the abdomen.

The homologies of the pulmonary segments in Arachnids.—On the accompanying page I have given a table representing

Table showing Homologies of the Abdominal Appendages and their Derivatives.

Somite.	Scorpiones.	Tetrapneumonous Araneæ.	Dipneumonous Araneæ.	Pedi palpi.	Japanese Limulus.
VIII	Genital operculum	First pair of lung- books	Pair of lung-books <sup>1</sup>	First pair of lung- books	Genital operculum.
IX	Pectines	Second pair of lung- books	Lateral tracheal trunks <sup>2</sup>	Second pair of lung- books	First pair of gill- appendages.
X	First pair of lung- books	A pair of spinners	A pair of spinners	—	Second pair of gill- appendages.
XI	Second pair of lung- books	A pair of spinners	A pair of spinners	—	Third pair of gill- appendages.
XII	Third pair of lung- books	—	—	—	Fourth pair of gill- appendages.
XIII	Fourth pair of lung- books	—	—	—	Fifth pair of gill- appendages.

<sup>1</sup> Represented in the Caponiidae by the anterior pair of tracheæ.<sup>2</sup> Represented in the Dysderida probably by the entire tracheal system, and in Argyroneta not at all.

the homologies of the abdominal appendages of the eighth to thirteenth somites in *Limulus* and the three pulmonate orders of Arachnida, based upon the most recent embryological researches. The segmental homologies given in this table agree with that of the same six somites given by Börner (:02, pp. 456, 457), and may be taken, so far as the pulmonate Arachnida are concerned, as sufficiently established, whereas the homologies of these segments in most of the Tracheate orders of Arachnida cannot be considered as satisfactorily established, since the necessary embryological evidence is wanting and that afforded by comparative anatomical research insufficient.

The most important point in connection with this question is the position of the genital opening.

(1) *Araneæ*.—I have shown in a previous paper ('95) that the genital ducts in *Attus floricola* are formed out of part of the cœlom of the pulmonary somite and open externally into the interpulmonary (epigastric) in-folding, which lies between the eighth and ninth somites. The genital segment in Dipneumonous spiders is, therefore, identical with the first pulmonary segment, which has been shown to be the eighth post-oral by all the most recent investigators (Kishinouye, '90; Simmons, '94; Jaworowski, '94; and myself, '95).

(2) *Scorpiones*.—Brauer ('95) has clearly shown that the seventh somite in the scorpions had been overlooked by previous authors, and that the genital operculum belongs to the eighth somite, the pectines to the ninth, and the four pairs of lungs to the tenth to thirteenth. Pereyaslawzewa (:07) also places the four pairs of lung-books in the tenth to thirteenth somites (pp. 174–176).

The homologies of the abdominal appendages in scorpions and spiders given in the table on p. 86 may, therefore, be considered as fully established by embryological evidence.

We have thus the remarkable fact, which I pointed out before ('95), that none of the lung-books in scorpions are actually homologous with the two pairs in spiders, and further, the two pairs of lung-books in spiders

are represented by external appendages in the adult scorpion, and the two anterior pairs of lung-books in the latter by external appendages in the adult spider. Now I cannot imagine that the pectines of scorpions could have been derived from appendages which had already sunk into the abdomen and been converted into lung-books, and the converse, that these external organs, after having lost their branchial nature and acquired new functions could ever have been converted in lung-books, is equally improbable. I consider, therefore, that the lung-books of the scorpions and those of the spiders must have been derived from branchiate appendages quite independently of each other, and that the terrestrial Arachnids are not monophyletic but must have had at least a diphyletic origin from primitive aquatic Arachnids with six pairs of abdominal branchiate appendages on the eighth to thirteenth somites.<sup>1</sup>

Laurie ('93) has expressed a similar opinion but based on palæontological grounds, that the lung-books in scorpions arose independently of those in other Arachnids.

(3) Pedipalpi.—It has been recently shown by Schimkewitsch (:06) that in the embryo of *Thelyphonus* the lung-books belong to the second and third abdominal somites (p. 43), while the genital opening is found between these two segments (pp. 63, 64), that is to say, exactly as in the *Araneæ*.<sup>2</sup>

<sup>1</sup> It is interesting to note in this connection that Schimkewitsch ('94, p. 207) discovered in the embryos of a scorpion on each side on the genital operculum three to four teeth (Warzen, *Km.*, fig. 12) which were formed on the same plan as those of the pectines but vanished again before birth. Schimkewitsch thinks it very probable that the genital operculum was once a sense organ like the pectines, and asks whether both were not once gills?

<sup>2</sup> Hansen ('93, p. 165) had previously pointed out that in *Thelyphonus* the first abdominal sternite should be sought for in the small sclerite at the anterior end of the abdomen, so that the large anterior sternite, which covers the genital opening and the first pair of lung-books, would, according to Hansen, belong to the second abdominal



Laurie and Gough, who examined embryos of Phrynids, are not quite clear as to the segmental position of the lung-books. Laurie ('94, p. 34) states that the first pair belongs either to the first or second abdominal somite, while the second pair belongs to the third somite. According to Gough (:02, p. 616) the lung-books belong to the first and second abdominal appendages, but the author does not say to which somites they belong. Pereyaslawzewa (:01), on the other hand, describes distinct paired appendages on each of the first five abdominal somites, the lung-books being formed from the third and fourth pairs (p. 194).

In view of the definite statements made by Schinkewitsch, as well as of the anatomical evidence afforded by the adult (see footnote on preceding page), and of the close relationship which the Pedipalpi bear to the Araneæ, we may accept as certain that the lung-books in the former group belong to the second and third abdominal segments, i. e. the eighth and ninth post-oral somites, and that the genital segment is the second and not the first of the abdomen, as stated by Laurie ('94). This would make the lung-books in the Pedipalpi directly homologous with the corresponding ones of the Araneæ, as represented in the table on p. 86.

I consider that the pulmonate Arachnids comprise two distinct groups, which have separately originated from branchiate ancestors, namely, (1) the Scorpiones, and (2) the Araneæ and the Pedipalpi. To the latter phylum some, if not all, of the remaining orders of tracheate Arachnida may perhaps be added, but I shall not at present enter further into the relationships of these other orders.

Pocock ('93) has already expressed the opinion that the Scorpiones, although the most primitive of all terrestrial Arachnida, could not have been the ancestors of any other orders of Arachnida, because the useful tail would not be likely to be lost. Pocock, who based this opinion on grounds segment. Recently Tarnani (:04, text-figs. on pp. 51, 52, and 121) and Börner (:02, :04) have also adopted this view.

which are totally different from mine, accordingly divides the Arachnida into two sub-classes, viz. (1) Ctenophora<sup>1</sup> for the scorpious, and (2) Lipoctena for the remaining terrestrial orders. Börner (:02, p. 459) in his paper on the segmentation and general classification of the Arachnida, accepts this subdivision, but on other grounds, viz., on account of the difference in the number of the segments of the meso- and metasoma which appear to exist between the Scorpiones and the Lipoctena. Börner, however, considers that both Scorpiones and Lipoctena must have been derived from a common ancestral group provided with at least five pairs of lung-books (pp. 459 and 463), but the difficulty (in my opinion almost an impossibility) of deriving a lung-book from a pectine, or vice versâ, does not seem to have occurred to him.

The question of the conversion of a sunken-in lung-book into the external spinners of the Araneæ would also present difficulties, but these do not appear to me nearly so great as in the case of the pectines, because the reconversion of the lung-septa (lamellæ) into external gill-like organs is not involved. I have, however, already pointed out that no trace of a lateral proliferation, corresponding to that of the pulmonary and tracheal sacs, is found in the embryo of *Attus floricola*, the entire post-appendicular invagination becoming the entapophysis in these two segments. Moreover, the spinning glands appear at quite an early stage (stage 5, *sp. g.*, fig. 6) at the apex of the appendages, which always remain recognisable as such to the end of the development. In fact, they have every appearance of having been directly developed into spinning organs from external appendages which were not sunken into the body, and, therefore, not lung-books.

So far as our knowledge goes, therefore, we may say that there is no evidence of any sort to indicate that the spinners of the Araneæ were derived from

<sup>1</sup> For which word the term Cteidophora has been substituted by Börner (:02, p. 465).

sunken-in lung-books, or that the spinner-segments ever possessed such organs in any ancestral form of this order.

When abdominal segments bearing spiracles in other Tracheate orders (Solifugæ, Pseudoscorpiones, Opiliones, and Acari) are homologised with those bearing spinners in Araneæ, as is done by Börner (:02, p. 457), the difficulty of deriving spinners from lung-books should be taken into account. For if the *Lipoctena* represent a natural group and the tracheæ leading from these spiracles are derived from lung-books, as is often assumed to be the case, it follows that the spinners in Araneæ must also have been derived from lung-books. But if we cannot admit the latter derivation, then either some or all of these tracheæ are not homologous with lung-books (i. e. they are new formations), or else the segments bearing them are homologous with the pulmonary segments in Araneæ (and not with those bearing spinners), or, finally, some or all of these orders may have originated independently of the Pedipalpi and Araneæ from branchiate ancestors (whether in connection with the Scorpiones or not is another question).

In the Solifugæ two (or at least one) of the three tracheate segments of the abdomen must be homologous with segments bearing spinners in Araneæ, and a knowledge of the development of the tracheæ would be necessary before one could determine the relationships of this order.

(4) *Limulus*.—According to Kingsley ('85) the genital segment in the American species of *Limulus* is the seventh post-oral segment, but Kishinouye ('91) has since discovered an additional somite between the last thoracic segment and the genital segment in the Japanese species, thus making the latter segment the eighth post-oral one. It is possible that this additional seventh somite was overlooked in the American *Limulus*, just as it has frequently been overlooked in the spiders and scorpions, for its presence would bring the segmentation of the abdomen of *Limulus* into line with that of spiders and scorpions.

Thus the homologies of the abdominal appendages in *Limulus* may with the greatest probability be represented as in the table on p. 86.

XI. HISTORICAL LIST OF PAPERS CONCERNING THE LUNG-BOOKS OF ARACHNIDS (EXCLUSIVE OF THOSE DEALING ONLY WITH ENERVATION, EMBRYOLOGY OR THEORETICAL CONSIDERATIONS.<sup>1</sup>)

Meckel ('09 and '10) gives the earliest anatomical description of the lung-books of a scorpion and spider. He observed the leaflets (sacculi) attached to a stalk (pedicel and ante-chamber) leading to the spiracle, and thought the stalk might be hollow. He looked upon the organ as a real gill-book.

G. R. Treviranus ('12, '16) describes the lung-books of scorpions and spiders (as true gills) and the interpulmonary fold and its muscles in spiders. He thought the "gills" may be mainly organs for absorbing moisture from the air, while the respiratory functions are carried out principally by four pairs of stigmata on the back of the abdomen (muscle impressions) and four pairs on the sides of the cephalothorax.

H. M. Gaede ('23) describes the four lung-books of a *Mygale* (as gills) and observed the "granulation" on the leaves. He thought the respiration took place, not in the "gill-leaves," but on the fine membrane behind them (i. e. on the posterior wall of the ante-chamber, which is smooth in some *Tetrapneumonous* spiders, e. g. in *Crypsidromus intermedius*).

Johannes Müller ('28A, '28E) discovered that the stalk (pedicel), ante-chamber and leaves (sacculi) in scorpions and spiders are hollow by blowing air into the spiracle, and so proved the pulmonary function of the lung-books. He

<sup>1</sup> The comparative anatomy of the lung-books is outside of the scope of this paper, so I give this list in the form of an appendix for the use of future workers on the subject, as it is more complete than any list yet given.

correctly surmises the passage of the blood between the saccules and denies the presence of blood-vessels. This is the most important description up to Leuckart's time.

H. Straus-Durckheim ('28) describes the lung-books of spiders, and says one may consider the saccules of these organs in Arachnids as non-ramified tracheal trunks, representing merely a continuation of the external integument in-folded into the interior of the spiracles (pp. 315-318).

J. F. Brandt ('33, p. 89) gives a poor description of the lung-books of *Epeira diadema* (as gills), apparently without knowledge of the work of the two previous authors.

A. Dugès ('36, p. 181) injected spiders' lung-books with carmine. There is also a note on the lung-books in Dugès, '38, p. 568, teste Duvenoy ('40, p. 465).

G. L. Duvenoy ('40) describes the lung-books of spiders.

J. van der Hoeven ('42) describes the lung-books of *Phrynus medius*,<sup>1</sup> calling them gills.

G. Newport ('43) describes the appearance of the lamellæ in scorpions and the circulation of the blood through the lung-books ("branchiæ") (pp. 295-297).

Pappenheim ('48) has a note on the lung-books of spiders.

A. Dugès ('49) gives figures of the lung-books of *Mygale* (Pl. ii, fig. 8, and Pl. iv, fig. 6), *Segestria* (Pl. iv, fig. 5), *Pholcus* (Pl. iv, fig. 7), and *Scorpio* (Pl. xviii, fig. 1f').

R. Leuckart ('49) describes the lung-books of scorpions and spiders. He discovered the spines of the ante-chamber in spiders and recognised the network on the leaves in scorpions as a chitinous thread on the surface of the membrane. He insists that lung-books are merely modifications of tracheæ (also '48, p. 119 note), and his paper is the most important that appeared before MacLeod's.

E. Blanchard ('49, '50) proved by injection that the blood passes through the septa and thence to the heart.

A. Menge ('51) describes the lung-books of *Argyroneta* (water spider). He failed to find any respiratory movements

<sup>1</sup> According to Kraepelin ('95, p. 41) v. d. Hoeven's species was in reality *Charon Grayi*, Gerv.

either in the lung-books or in the enclosed air, and observed that the entire cuticula of these organs is shed at moulting. He doubted their respiratory function.

F. Leydig ('55) found that the "granulations" observed by previous authors in the lung-leaves of spiders are really internal processes, like those in the posterior tracheæ.

L. Dufour ('56) describes the scorpion's lung-books (pigment and reticulation of the leaves, etc.).

E. Claparède ('63) describes the circulation of the blood, with some notes on the lung-leaves, in the spider.

P. Bertkau ('72) gives a good description of the lung-books in spiders, and the earliest account of their growth in young spiders.

C. Chun ('76), from a brief remark (p. 42), evidently implies that he has found an epithelium with regular cell-boundaries on the lung-leaves of Arachnids, but reserves the proof for a later occasion.

H. Lebert ('77, p. 25) makes some very curious observations, such as his discovery of a second pair of smaller lung-books (Nebenfächertracheen) in other spiders besides *Tetraneumon*es (e. g. in some *Argiopidae*); also bifurcate saccules.

J. MacLeod ('80, '82, '84) advanced our knowledge greatly beyond the works of his predecessors by the use of sections. In his first paper ('80) he describes the lung-books as "*un faisceau de trachées aplaties, foliiformes*" (p. 48), but influenced later by the branchial theory he re-casts his method of treating the subject ('82, '84). His principal paper ('84) is, perhaps, the best known of all works on the lung-books.

E. Ray Lankester ('81, '85a, '85b) in his first paper compares the lung-books of scorpions with the gill-books of *Limulus* from actual preparations, and derives lung-books from gill-books by a theory. This paper ('81) affected most subsequent studies of the subject, and made the development and comparative anatomy of the respiratory organs a subject of paramount interest in the Arachnida. His later papers ('85a, '85b) describe the circulation of the blood through the



lung-books, and the histology of the lamellæ in *Scorpio*, and a new theory of the origin of the lung-books.

P. J. Mitrofanof ('81) makes some remarks on the lamellæ in *Argyroneta* (teste Schimkewitsch '84, p. 64).

W. Schimkewitsch ('84) describes the lung-books of *Epeira*, without knowledge of MacLeod's principal paper ('84).

F. Plateau ('86) searched for respiratory movements in living *Scorpiones*, *Araneæ*, and *Opiliones*, with negative results.

W. Wagner ('88) describes the moulting and growth of the lung-books in immature spiders.

L. Berteaux ('89) describes minutely the lung-books of spiders and scorpions. This paper is the most complete on the histological structure, particularly that of the cuticular formations, and various errors made by MacLeod ('84) in this respect are corrected. (His description of the form of the lung-leaves and the ante-chamber is, however, unsatisfactory, and is improved upon by Schneider ['92].)

J. Tarnani ('89) figures the topography of the two pairs of lung-books in *Thelyphonus*, and describes the interpulmonary folds. In his later work (:04) these lung-books are also figured and described (p. 121).

C. Vogt ('89) gives an original description of the lung-books of *Epeira diadema*.

A. Schneider ('92) describes the circulation of the blood through the lung-books, and gives an account of the general structure of these latter organs in spiders. This very excellent paper is indispensable as a supplement to Berteaux's important histological work.

M. Laurie gives an account of the structure and histology of the lung-books in *Pedipalpi* ('94), and of the difference in the chitinous armature of the septa in different groups of scorpions ('96a, 96b).

Sophie Pereyaslawzewa (:01) figures some sections of the lung-books of *Phrynidæ* (figs. 59, 62 and 64), and gives a number of descriptive notes, especially on the histology of the septa and on the pulmonary muscles (pp. 251-262).

A. Börner (:04) gives an account of the lung-books in Pedipalpi, and some diagrams to illustrate their structure in Arachnids generally.

#### LIST OF LITERATURE.

(The titles of papers which I have not seen are enclosed in brackets.)

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- '93a. ——— "Notes on the Chernitidæ, with Special Reference to the Vestigial Stigmata and to a New Form of Trachea," 'Journ. Linn. Soc. London,' Zool., xxiv, pp. 410-430, Pls. xxxi and xxxii, 1893.
- '93b. ——— "Additional Notes on the Origin of the Tracheæ from Setiparous Glands," 'Ann. Mag. N. H.,' (6), xi, pp. 24-28, 1893.
- '94. ——— "Vestigial Stigmata in the Arachnida," 'Ann. Mag. N. H.,' (6), xiv, pp. 149-153, 3 text-figs., 1894.
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## EXPLANATION OF PLATES 1—7,

Illustrating Mr. W. F. Purcell's paper on "Development and Origin of the Respiratory Organs in Araneæ."

## STAGES IN THE DEVELOPMENT.

Stage 1 (*St. 1*), just before the appearance of the pulmonary furrows : figs. 4, 7, and 7A (all from same embryo).

Stage 2 (*St. 2*), with two pulmonary furrows : figs. 1, 5, 5A, 8, and 8A-8H (5, 5A, 8, 8A-8H all from one embryo) ; figs. 9, 10, 14.

Stage 3 (*St. 3*), with three pulmonary furrows : figs. 2, 11.

Stage 4 (*St. 4*), with 4-5 pulmonary furrows : figs. 12, 15.

Stage 5 (*St. 5*), with 5-6 pulmonary furrows : figs. 3, 6, 6A, and 27 (6, 6A, and 27 from one embryo) ; figs. 13, 13A, and 13B (all from one embryo) ; figs. 16, 16A-16E, 35, and 35A (all from one embryo).

Stage 6 (*St. 6*), after end of reversion and shortly before hatching : figs. 17 and 43 (from same embryo) ; figs. 18, 28, 41.

Stage 7 (*St. 7*), after hatching : fig. 34.

Stage 8 (*St. 8*), after first post-embryonic moult : figs. 29 and 29A (from same embryo) ; fig. 30.

## ABBREVIATIONS FOR ALL THE PLATES.

The yolk is coloured yellow in the figures representing sections, all of which have been drawn with the aid of a drawing apparatus. The letters (*St. 1*), (*St. 2*), etc., alongside the numbers of the figures denote the stage of the embryo from which the section has been made.

*a. ob. m.* 8 and 10. Anterior oblique muscles of somites 8 and 10. *a. spin.* Inner openings of anterior pair of spinners. *ab. app.* 1-4. Abdominal appendages 1-4. *ant.* Anterior side. *ap.* Apical pouch of horn of pulmonary sac in developed lung-book. *app.* 6. Sixth prosomatic appendage. *ar.* 7-11. Areas in contact with the ends of the segments of the ventral longitudinal muscles of somites 7-11 at the time of the formation of the entochondrites. *b.f.* Basal fold of tracheal trunk. *bd. c.* Blood-corpuscles. *br.* Branches of tracheal trunk. *c.* Cones of a chitinous saccule. *can.* Canal of communication. *cent.* Centre of section. *cl. 1*, *cl. 2.* Clefts on the distal side of first and second pulmonary saccules. *cæl.* 6-14. Cœlomic sacs of 6th-14th post-oral somites. *cu.* Cuticula. *cu.'*, *cu''* Cuticula formed at first and second post-embryonic moults. *d. l. m.* 8-15. Segments of the dorsal longitudinal muscles in somites 8-15. *d. v. l. m.* Longitudinal muscle alongside of the proctodæum uniting the last segment of the dorsal with that

of the ventral longitudinal muscles. *d. v. m.* 7-10. Dorso-ventral muscles behind somites 7-10. *dist.* Distal side. *dors.* Dorsal side. *dors. (lat.)*. Dorsal (originally lateral) side. *ec. g. d.* ectodermal portion of genital duct. *ec. t.* 8-11. Ectodermal tendons (entapophyses, apodemes) of the appendages of the 8th-11th somites. *end.* Eudoderm. *ep.* epithelium. *f. 1, f. 2, etc.* First, second pulmonary furrows, etc., in the order of their formation. *g.* Genital cord. *g. o.* Genital opening into interpulmonary fold (to the outside in fig. 40). *gr.* Groove behind abdominal appendages. *h.* Horn (procurved end) of pulmonary sac. *horiz. pl.* Horizontal plane of body. *hy.* Hypodermis. *hy'*. Fibrous parts of the hypodermis of the ectodermal tendons. *inf.* Infolding of the hypodermis. *interp. fld.* Interpulmonary (epigastric) fold or its rudiment. *l.* Lumen. *l. spin. m.* 10. Lateral muscle to anterior side of first spinner (in 10th somite). *l. tr.* Lateral trunks of tracheal system. *lae.* Lacuna. *lat.* Lateral side. *lb.* Lung-book or tissue forming it. *m.* Muscles or tissue forming them. *m. spin.* Inner openings of middle pair of spinners. *m. spin. m.* 10. Medial muscle to anterior side of first spinner (in 10th somite). *m. tr.* Medial trunks of tracheal system. *ma.* Matrix cells. *med.* Medial side. *med. pl.* Median plane. *mes. g. d.* Mesodermal part of genital duct. *nv. g.* Nervous ganglion of the pulmonary somite. *op.* Opening at anterior end of abdomen. *p. ob. m.* 8-11. Posterior oblique muscles of somites 8-11. *p. spin.* Inner openings of posterior pair of spinners. *ped.* Pedicel. *post.* Posterior side. *pr. ax.* Principal axis of appendage. *proc.* Proctodæum. *pulm. l.* Lumen of pulmonary sac. *pulm. prol.* Pulmonary proliferation or growing end of pulmonary sac. *pulm. s.* Pulmonary sac. *rd.* Chitinous thickening on lateral side of tracheal pedicel. *s., s. 1, s. 2, etc.* Pulmonary sacculæ; first, second sacculæ, etc., in the order of their formation. *s'.* New chitinous sacculæ forming before the first post-embryonic moult. *seg. t.* 8-11. Segmental tubes of 8th-11th somites. *sl.* Slanting medial part at base of posterior wall of first appendage. *sp.* Spiracle. *sp. g.* Spinning gland. *spi.* Anastomosing spines. *spin. m.* 10. Muscles to the anterior side of first pair of spinners. *spz.* Sperma. *st. p.* Stercoral pocket. *t.* Mesodermal tendon (entochondrite). *t.* 7-11. Entochondrites at hind ends of the segments of the ventral longitudinal muscles of somites 7-11. (*t.* 8-11.) Indicates the position of these tendons, where not drawn in. *tr.* Tracheal trunk. *tr. l.* Lumen of tracheal plate or sac. *tr. m.* Transverse muscle on lateral side of tracheal pedicel. *tr. pl.* Tracheal plate. *tr. prol.* Tracheal proliferation. *tr. s.* Tracheal sac. *tr. tub.* Tracheal tubules or finest branchlets. *v. l. m.* 7-11. Segments of the ventral longitudinal muscles in somites 7-11. *v. sin.* Ventral sinus of abdomen. *vc.* Vacuole. *vent.* Ventral side. *vent. (med.)*. Ventral (originally medial) side. *vest.* Vestibule. *vit.* Vitellophagous cell. *w.* Two-celled column. *x.*

Point at which the entochondrite is attached to the hypodermis. *y*. Three-celled column. *z*. Pavement cell. *w*. *x*. *x'*. *y'*. and *y'*. *z'*. Anterior, distal, and posterior sides of appendage.

## PLATE 1.

### Embryology of *Attus floricola*.

[Longitudinal sections are cut parallel to the principal axis (*pr. ax.* in figs. 1-3) of the appendage and at right angles to the posterior margin of the latter. Transverse sections are parallel to the principal axis and to the posterior margin.]

Figs. 1-3.—(Zeiss obj. C, oc. I, hot alc. subl.) Transverse sections showing the change of position of the first pair of abdominal appendages during the reversion of the embryo. Fig. 1 represents the stage with two pulmonary furrows, fig. 2 with three, and fig. 3 with four, five, or more furrows.

Fig. 4.—(Zeiss C, III, hot alc. subl.) Longitudinal section through the lateral region of the four abdominal appendages, just previous to the appearance of the pulmonary furrows and the commencement of the reversion.

Figs. 5 and 5A.—(Zeiss C, III, hot alc. subl.) Longitudinal sections through the abdominal appendages at the stage with two pulmonary furrows (*f. 1, f. 2*), corresponding to fig. 1. Fig. 5 passes through the medial, fig. 5A through the lateral region of the anterior appendages.

Figs. 6 and 6A.—(Zeiss C, III, hot alc. subl.) Longitudinal sections through the abdominal appendages at the stage with five or six pulmonary furrows, corresponding to fig. 3. Fig. 6 passes through the medial, fig. 6A through the lateral region of the appendages.

Figs. 7 and 7A.—(Zeiss  $\frac{1}{2}$  oil im., II, hot alc. subl.) Longitudinal sections through the medial (fig. 7) and lateral part (fig. 7A) of the first abdominal appendage (enlarged from the same embryo as fig. 4) just before the formation of the pulmonary furrows; *ep.*, epithelium (belonging to somite 9) behind first appendage.

## PLATE 2.

### Embryology of *Attus floricola*.

[Longitudinal sections are cut parallel to the principal axis (*pr. ax.* in fig. 1) of the appendage.]

Fig. 8.—Diagrammatic view of the posterior side of the first abdominal appendage at the end of the stage (corresponding to fig. 1 with two pulmonary furrows, *f. 1, f. 2*) (from a wax reconstruction). The parallel lines represent the planes of sections; *ep.*, the epithelium

represented as cut along the groove (*gr.*) in figs. 8A-8D, and along the deepest part of the pulmonary sac (*pulm. s.*) in figs. 8F and 8G.

Figs. 8A-8H.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Longitudinal sections through the first abdominal appendage, of which fig. 8 is a reconstruction. Figs. 8A-8E pass through the medial and 8F-8H through the lateral halves of the appendage, and their positions are indicated in fig. 8; *ep.*, epithelium (belonging to somite 9) behind the first abdominal appendage.

### PLATE 3.

#### Embryology of *Attus floricola*.

[Longitudinal sections are cut parallel to the principal axis (*pr. ax.* in figs. 1-3) of the appendage.]

Figs. 9 and 10.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Longitudinal sections (from different embryos) through the medial region of the first abdominal appendage at the commencement (fig. 9) and the end (fig. 10) of the stage with two pulmonary furrows; *ep.*, epithelium (belonging to somite 9) behind first appendage.

Fig. 11.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Section through the medial region of the first abdominal appendage at about the commencement of the 3-furrow stage, cut at a slight inclination to the longitudinal axis of the appendage.

Fig. 12.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Longitudinal section through the lateral region of the first abdominal appendage at the stage with four to five pulmonary furrows.

Figs. 13-13B.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Transverse sections cut parallel to the anterior side of the first abdominal appendage at a stage with at least five well-developed pulmonary furrows, fig. 13 being the second, 13A the fifth, and 13B the eighth section from the posterior side of the appendage (13 and 13A are in outline and show ectodermal tissue only). *sp.* The primitive spiracle; *s.* 1-s. 5, the five oldest saccules.

Fig. 14.—Sketch of first abdominal appendage of the right side at the stage with two pulmonary furrows, from a wax reconstruction, seen from behind and distally.

Fig. 15.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Sagittal section (cut parallel to the median plane of the embryo, c.f. fig. 2) through the first abdominal appendage at the commencement of the stage with four pulmonary furrows (slightly later than fig. 2).



## PLATE 4.

Embryology of *Attus floricola*.

[Longitudinal sections are cut parallel to the principal axis (*pr. ax.* in fig. 3) of the appendage.]

FIG. 16.—Diagrammatic view of the posterior side of first abdominal appendage at the stage with five well-developed pulmonary furrows (corresponding to fig. 3) from a wax reconstruction. The parallel lines represent the planes of section; *ep.*, the epithelium represented as cut along the line marked (*ep.*, fig. 16) in figs. 16A–16D.

FIGS. 16A–16E.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Longitudinal sections through the first abdominal appendage, of which fig. 16 is a reconstruction.

FIG. 17.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Transverse section through first abdominal appendage shortly before the hatching of the embryo, cut along the line indicated in fig. 18.

FIG. 18.—(Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Sagittal section of the same stage as fig. 17 and cut along the line indicated in the latter figure.

## PLATE 5.

FIG. 19.—(Zeiss  $\frac{1}{12}$  oil im., I.) Sagittal sections through the cuticula of the lateral part of the interpulmonary fold (between the entapophysis and the lung-book), or its rudimentary remains in A, *Lycosa* sp.; B, *Philodromus fuscmarginatus* (subadult); and C, *Argyroneta aquatica* (adult ♂). The sections are all arranged in the same positions.

FIG. 20.—(Caustic potash.) *Attus* sp. (adult). Chitinous skeleton of abdomen anterior to the pulmonary spiracles, drawn from behind. The posterior wall of the ante-chamber has been removed on the right side, and on the left the grate-like openings are visible through this wall.

FIG. 21.—(Caustic potash.) *Tegenaria domestica* (ad. ♀). Chitinous skeleton of abdomen from above.

FIG. 22.—(Zeiss  $\frac{1}{12}$  oil im., I, picro-sulphuric acid.) *Attus floricola* (mature, or nearly mature ♀). Sagittal section through the interpulmonary fold between the lung-book and the entapophysis, showing the cuticula only.

FIG. 23.—(Zeiss  $\frac{1}{12}$  oil im., I, Flemming's sol.) *Attus floricola* (ad. ♂). Sagittal section through the interpulmonary fold and the entapophysis in the region indicated in fig. 20.

Figs. 23A and 23B.—Similar sections of the same ♂ in the regions indicated in fig. 20. Fig. 22A shows the cuticula only.

Fig. 24.—(Zeiss  $\frac{1}{2}$  oil im., IV.) *Linyphia triangularis* (ad. ♂). Sagittal section through the vestibule of the trachea in the region indicated in fig. 25, showing the cuticula only.

Fig. 25.—(Zeiss C, IV, caustic potash.) *Linyphia triangularis* (ad. ♀). Cuticular skeleton of basal region of tracheal system.

Fig. 26.—The same as fig. 24, but in the median plane along the line indicated in fig. 25.

## PLATE 6.

### Adult or sub-adult spiders.

Fig. 27.—(Zeiss F, I, hot alc. subl.) Embryo of *Attus floricola* at the stage with 5-6 pulmonary furrows. Reconstruction (made from the same series of sections as figs. 6 and 6A) of the right pulmonary and tracheal appendages seen from their inner side. The only mesodermal elements shown are the two segmental tubes, *seg. t.* 8 and 9. The basal outlines of appendages 1-3 are indicated by dotted lines, as are also the lumens of the pulmonary and tracheal sacs.

Fig. 28.—(Zeiss F, I, hot aqueous subl.) Embryo of *Attus floricola* after the reversion. Reconstruction from transverse sections of the rudimentary trachea, together with the muscles and entochondrites attached to the right half. The sketch is imagined as taken directly from above, the anterior part being therefore higher in the figure than the posterior part (cf. also figs. 41 and 43 of the same stage). The rudimentary lumen is outlined by the dotted line.

Fig. 29.—(Zeiss F, I, hot alc. subl.) Young *Attus floricola*, after the first post-embryonic moult. Reconstruction of the tracheal system (imagined as taken directly from above) together with the muscles and entochondrites connected with the right half and some of those on the left. 29A (Zeiss  $\frac{1}{2}$  oil im., IV). Transverse section through a right medial trunk at the line indicated in fig. 29.

Fig. 30.—(Zeiss  $\frac{1}{2}$  oil im., II, hot alc. snbl.) Young *Agelena labyrinthica* just before the second post-embryonic moult. Sagittal section through a lateral tracheal trunk and the hypodermis below it; the cuticula of the second moult is already formed.

Fig. 31.—(Zeiss C, III, caustic potash.) *Attus floricola* (ad. ♀). Tracheal system. (The terminal portions of the secondary tubules are not drawn in.)

Fig. 32.—(Zeiss C, III, equal parts of Flemming's sol. and abs. alc.)

*Segestria senoculata* (ad. ♀). Obliquely transverse section cut at an angle of  $38^{\circ}$  to the horizontal (cf. fig. 33) through the basal part of a tracheal trunk (combined from a couple of sections).

Fig. 33.—Similar to the last but a sagittal section, showing the entapophysis cut across the line indicated in fig. 32.

Fig. 34.—(Zeiss  $\frac{1}{2}$  oil im., IV, Flemming's sol.) Embryo of *Teegenaria atrica*, just after hatching. Transverse section through two upper pulmonary saccules.

## PLATE 7.

Figs. 35 and 35A.—(Zeiss  $\frac{1}{2}$  oil im., II, hot alc. subl.) Embryo of *Attus floricola* at the stage with five pulmonary furrows (from the same series of sections as figs. 16–16E). Longitudinal sections through the tracheal appendage along the lines indicated in fig. 27.

Fig. 36.—(Zeiss  $\frac{1}{2}$  oil im., I.) *Crypsidromus intermedius*. Sagittal section through the rudimentary entapophysis or muscular stigma of the first pulmonary sternite, showing the distal part of some of the long hypodermal fibres (*hy.*<sup>1</sup>) to which the entochondrite of the pulmonary segment is attached.

Figs. 37 and 37A.—(Zeiss  $\frac{1}{2}$  oil im., I. alc.) *Palpimanus* sp. Transverse sections through the anterior (fig. 37) and the posterior (fig. 37A) regions of the median entapophysis of the tracheal system.

Fig. 38.—(Zeiss C, IV, caustic potash.) *Scytodes testudo*. Basal part of chitinous skeleton of the tracheal system.

Fig. 39.—(Zeiss  $\frac{1}{2}$  oil im., IV, alc.) *Scytodes testudo*. Transverse section through the cuticular lining of the median entapophysis of the tracheal system along the line indicated in fig. 38.

Fig. 40.—(Zeiss  $\frac{1}{2}$  oil im., I.) *Harpactes Hombergi* (ad. ♂). Median sagittal section through the cuticula of the interpulmonary fold and the genital opening.

Fig. 41.—(Zeiss C, II, hot alc. subl.) Embryo of *Attus floricola* after the reversion in sagittal section, showing the principal muscles, ectodermal and mesodermal tendons and segmentation of the abdomen (combined from several sections). The lungs, genital cords, and the stercoral pocket (imagined as seen from the medial side) are drawn in to show their topography, the last being represented in median section. The muscle (*p. ob. m.* 8) is the only one lying between the genital duct (*g.*) and the lung-books (*lb.*).

Fig. 42.—(Zeiss A, II, caustic potash.) *Tegenaria domestica* (adult). Portions of the pair of median tracheal trunks, showing the

place of attachment to the entochondrite (seen from the dorsal side). A, part of left trunk; B, anterior part of right trunk (see fig. 21).

Fig. 43. — (Zeiss  $\frac{1}{12}$  oil im., II, hot alc. subl.) Embryo of *Attus floricola* after the reversion. Transverse section through the ventral sinns of the abdomen in the region of the tracheal plate (along the line indicated in fig. 28; same stage as figs. 28 and 41).